UNIVERSITY OF CALIFORNIA

Santa Barbara

Assessing Marine Resources Using Ecology, Fisheries Science, and Expert Judgment

A dissertation submitted in partial satisfaction of the

requirements for the degree Doctor of Philosophy

in Ecology, Evolution and Marine Biology

by

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ACKNOWLEDGEMENTS

Thank you to my advisor, Steve Gaines, for your guidance, support, and generosity. Your enthusiasm and ability to provide feedback on a broad range of scientific subjects is remarkable. Thank you to my committee, Bob Warner, Jenn Caselle, and Scott Hamilton, for your quality scientific advice. Bob, I really enjoyed working with you during the NCEAS distributed graduate seminar and appreciated our conversations during the class and later with my research. Jenn and Scott, thank you for your comments on my thesis, which has been greatly improved by your expertise in kelp forest ecology. Also, without your logistical assistance with field work, much of my thesis would not have been possible. Thank you to Nick Shears, who I consider an honorary member of my committee; he has given me tremendous guidance and encouragement from the initial stages of broad ideas, questions, and planning through to the final stages of analyses and writing.

Thank you to the numerous undergraduate assistants who volunteered in the lab and in the field, especially Roni Shen and Micki Adams for your bright spirits and commitment to assisting with my labwork during most of my graduate career. Shen Meinhold, Weiman Meinhold, Olivia Turnross, Anastasia Quintana, and Thea Rogier also made a dedicated effort assisting me during several quarters. A big thanks to Claudia Scianna, who spent much of her time as a visiting graduate student from Italy assisting me in the lab with such a positive attitude. Thank you to UCSB's Research Mentorship Program and my high school student assistants.

All three of my thesis projects benefited greatly from a fabulous group of collaborators and colleagues. I spent my first years at UCSB working with a great team at NCEAS led by Ben Halpern, Carrie Kappel, Fio Micheli, and Kim Selkoe. Thank you for the opportunity to lead this project that entailed interviewing about 75 scientific experts working within the California Current. The interviews and interactions with our interdisciplinary group of co-authors served as a great introduction to the west coast ecological and scientific community.

My ecological research at the Channel Islands would not have been possible without the tireless efforts of UCSB's Partnership for Interdisciplinary Studies of Coastal Oceans (PISCO) scientific dive team, in particular Katie Davis and Avrey Parsons-Field. Thank you to Libe Washburn and David Salazar for maintaining UCSB's PISCO moorings and all the many PISCO students and technicians who conducted field work. Thanks to Chris Gotschalk for summarizing PISCO's temperature data.

Thank you to Sarah Rathbone who offered not only many hours of assistance at the docks and lab but also immense enthusiasm to the project. I am grateful to Jorge Cornejo-Donoso, who patiently assisted me with database and analysis work and bolstered my confidence in working with R on my own. Thank you to Rebecca Toseland for assistance with the economics side of the fishery and for your positive attitude. Thank you to Tal Ben-Horin for offering wonderful advice on several analyses with patience and ease. Thank you, Tom Bell, for summarizing wave data and great feedback on kelp forest dynamics and, Dave Kushner with the Channels Islands National Park's Kelp Forest Monitoring Program, for providing red sea urchin size structure data. Thank you to Jeremy Claisse for summarizing satellite sea surface temperature data and for helpful conversations about sea urchins.

My work investigating the Santa Barbara commercial sea urchin fishery was an important way of integrating my research into the local Santa Barbara community. Thank you to the

many fishermen who participated in this study. While I cannot list your names here due to confidentiality agreements, it was a pleasure interacting with all of you on the Navy Pier in Santa Barbara. After long dive trips sometimes in rough conditions, I was often greeted with big smiles and a willingness to participate in my research. Special thanks go out to Stephanie Mutz, president of the Commercial Fishermen of Santa Barbara (CFSB), who initiated sampling efforts at the port of Santa Barbara, and for helpful information about the fishery. Thank you to former president of CFSB, Harry Liquornik, for useful conversations about my project and insights into the sea urchin industry. This research would not have been possible without the cooperation of the weigh-masters, especially Wes Carpenter, and the assistance from the Santa Barbara Fish Market, especially Brian Colgate. Thank you to Dave Rudie from Catalina Offshore Products for price data, quality data, and information from the industry side of the fishery. Thanks to Jeremy Prince for his scientific perspective on the fishery and for his recommendations of research needs, specific to the California sea urchin fishery. Thank you to Pete Kalvass from California Department of Fish and Wildlife for providing the commercial sea urchin data and engaging in insightful conversations about the fishery.

Thank you to the Gaines lab, Hofmann lab, Warner lab, PISCO lab, and the students, staff, and faculty from the Department of Ecology, Evolution and Marine Biology, the Marine Science Institute, and the Bren School of Environmental Science and Management. Thank you to the Henry Luce Foundation and the Luce Environmental Science to Solutions Fellowship Program for both financial and academic support. Thank you to the Ezal family for the inspirational Nejat B. Ezal Memorial Fellowship Award. This study utilized data collected by the PISCO, a long-term ecological consortium funded by the David and Lucile Packard Foundation and the Gordon and Betty Moore Foundation.

Deep thanks go to Jim Carlton, who initially encouraged me to enter the field of marine ecology during my time at the Williams-Mystic program in 2000. He has been a steadfast, scientific advisor, since we met, providing countless hours of valuable insight and encouragement to me. I appreciate his genuine inspiration, warmth, energy, creativity, and generosity. Thank you to my friends for conversations about science and for their network of love and support, especially during the times when I needed it most. Thank you to my meditation and yoga community—I have learned so much from our shared practice that has not only helped me complete this thesis but also enriched my life immeasurably. Thank you, Myrna Teck and Loren Amdursky for your love and support. Thank you, Patricia Teck Seggerman for being a loving and supportive sister—you have also played numerous other roles in my life including: parent, nurse, advisor, lawyer, and best friend. I am grateful to my parents, Bruce and Susan Teck; your spirits will always live within me as a source of strength and love to continue following my dreams. And, I am deeply grateful to my husband, Julio Lorda Solórzano; your loving kindness and patient nature, whether in the lab, office, hospital, or home have not only made this dissertation possible but also supported a life I am honored to share with you. Last but not least, thank you Sebastián Jay. I am so grateful for your inquisitive, determined, and playful outlook on life and learning. Spending time with you has renewed my vigor for conducting science from this point of view.

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ABSTRACT

Assessing Marine Resources Using Ecology, Fisheries Science, and Expert Judgment

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Proquest Abstract (150 word limit)

One of the most challenging issues facing resource managers is how to prioritize conservation goals within ecosystems. Firstly, I found experts primarily used percent change and trophic impact as the basis for assigning ranks to ecosystem impacts. Mudflats, beach, salt marshes, and rocky intertidal were judged most vulnerable, and the highest stressor rankings included invasive species, ocean acidification, sea temperature change, and demersal destructive fishing. Secondly, I investigated how demographic metrics of the red sea urchin *Mesocentrotus franciscanus* varied in response to protection, temperature, and the giant kelp *Macrocystis pyrifera*. Thirdly, I demonstrated that urchin reproduction can predict fishing industry's standard quality ratings, price, effort, and landings. Understanding the spatiotemporal dynamics of urchin's reproduction is not only useful in understanding the ecology and population biology of this species, but also it is essential for managers and policymakers to direct efficient management and ensure sustainability, particularly under future climate change scenarios.

General Abstract (no word limit)

One of the most challenging issues facing resource managers is how to prioritize conservation goals within ecosystems. Although opinion does not replace empirical data, synthesizing expert opinion can reveal areas of agreement, where scientific data may be vast, and areas of disagreement, often where scientific information is lacking. In Chapter 1 (*Using expert judgment to estimate marine ecosystem vulnerability in the California Current*), using the California Current as a case study, I gathered, quantified, and critically examined expert opinions evaluating potential stressors (n=53) within marine ecosystems (n=19). Experts (n=107) ranked human activities and performed an exercise to help quantify how they use particular vulnerability criteria to rank impacts. Results indicated that experts primarily (89%) used percent change and trophic impact as the basis for assigning ranks. Four intertidal ecosystems (mudflats, beach, salt marshes, and rocky intertidal) were judged most vulnerable to the stressors evaluated. The highest stressor rankings included invasive species, ocean acidification, sea temperature change, and demersal destructive fishing. These results provide a quantitative, transparent, and repeatable assessment of relative vulnerability across ecosystems to any ongoing or emerging human activity. Combining these results with data on the spatial distribution and intensity of human activities could offer a systematic foundation for ecosystem-based management.

Focusing on a smaller spatial scale and investigating empirical data of particular impacts are necessary to support management decisions with greater certainty. Marine protected areas arrayed over a biogeographic cline provided an opportunity to test the potentially interactive effects of protection from fishing with other spatial drivers of demographic variability. In Chapter 2 (*Disentangling the effects of fishing and environmental forcing on demographic variation in an exploited species*), I used a network of MPAs established in 2003 in the

Channel Islands to investigate the effects of fishing on one of the most important exploited species in California, the red sea urchin *Mesocentrotus franciscanus* (previously *Strongylocentrotus* A. Agassiz, 1863). This multi-million dollar industry relies on the reproductive organ of the species as a fresh sushi product both domestically and internationally. Since spatially explicit ecological information is essential to understand for proper management, I described spatial demographic patterns in red sea urchins within the northern Channel Islands, where almost half of California's landings and value originate. I investigated how reproductive condition and other urchin demographic metrics varied in response to protection (MPA vs unprotected areas), sea temperature, and the main food source, the giant kelp *Macrocystis pyrifera*. Biomass and mean size of red sea urchin adults were greater within MPAs, and consequently reproductive biomass was elevated in non-fished locations. Kelp density was an important explanatory variable of all red sea urchin demographic traits (size, gonadosomatic index [GSI], density, biomass, and reproductive biomass) and as a main effect accounted for a significant amount of variability in size and GSI. In addition, red sea urchin adult size and reproductive biomass were higher in the western, cooler region. A number of complex interactions were observed, notably urchin adult biomass and reproductive biomass were positively related with kelp but only in warmer areas within the region. Our results underscore the significant impacts from humans as predators and that marine protected areas can benefit fished herbivores, but herbivore demographics are also tightly linked with macroalgal dynamics embedded in a complex temperature gradient.

Within this multi-million dollar red sea urchin fishing industry, the primary driver of fishing as in many other fisheries is price, which is in turn determined by gonad quality. A relatively simple measure of the fraction of the body mass that is gonad, the GSI, provides

important insight into the ecological and environmental factors associated with spatial and temporal variability in reproductive quality, and hence the value of the fishery. In Chapter 3 (*Quality of a fished resource: Assessing spatial and temporal dynamics*), I examined patterns of GSI showing a clear annual cycle and revealed GSI as a tool to predict the industry's standard quality ratings, price, fishing effort, and fishing landings. Understanding the spatiotemporal dynamics of urchin's reproduction is not only useful in understanding the ecology and population biology of this species, but also it is essential for managers and policymakers to direct efficient management and ensure sustainability, particularly under future climate change scenarios.

Changes in climate (e.g., increases in temperature, storm severity, and storm frequency) may result in both profound ecological ramifications and varying human behavior. For example, if storms increase during the winter, fishing effort during the high quality resource season may be more limited. If the higher frequency of storms and increased wave action reduces macroalgal density, the quality of a fished resource may be degraded in certain areas that were once important fishing grounds. In addition, since climate and fishing both influence species' distribution and abundance, it is important to understand their combined effects on the system may be synergistic. Examining phenological changes in species, which may include tracking reproduction over seasons and years, is not only important for resource management but also may be a simple ecological indicator of climate change.

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I. Using expert judgment to estimate marine ecosystem vulnerability in the California Current[1]

Collaborators: Benjamin S. Halpern, Carrie V. Kappel, Fiorenza Micheli, Kimberly A. Selkoe, Caitlin M. Crain, Rebecca Martone, Christine Shearer, Joe Arvai, Baruch Fischhoff, Grant Murray, Rabin Neslo, and Roger Cooke

1 Published in 2010. *Ecological Applications* **20**: 1402-1416.

Abstract

As resource management and conservation efforts move towards multi-sector, ecosystem-based approaches, we need methods for comparing the varying responses of ecosystems to the impacts of human activities in order to prioritize management efforts, allocate limited resources, and understand cumulative effects. Given the number and variety of human activities affecting ecosystems, relatively few empirical studies are adequately comprehensive to inform these decisions. Consequently, management often turns to expert judgment for information. Drawing on methods from decision science, we offer a method for eliciting expert judgment to (1) quantitatively estimate the relative vulnerability of ecosystems to stressors, (2) help prioritize the management of stressors across multiple ecosystems, (3) evaluate how experts weight different criteria to characterize vulnerability of ecosystems to anthropogenic stressors, and (4) identify key knowledge gaps. We applied this method to the California Current region in order to evaluate the relative vulnerability

of 19 marine ecosystems to 53 stressors associated with human activities, based on surveys from 107 experts. We found that 89% of the variance in experts' judgments of vulnerability across all 19 ecosystems can be explained by two criteria: the ecosystem's resistance to the stressor and the number of species or trophic levels affected. Four intertidal ecosystems (mudflats, beach, salt marshes, and rocky intertidal) were judged most vulnerable to the suite of human activities evaluated here. The highest vulnerability rankings for coastal ecosystems were invasive species, ocean acidification, sea temperature change, sea level rise, and habitat alteration from coastal engineering, while offshore ecosystems were assessed to be most vulnerable to ocean acidification, demersal destructive fishing, and shipwrecks. These results provide a quantitative, transparent, and repeatable assessment of relative vulnerability across ecosystems to any ongoing or emerging human activity. Combining these results with data on the spatial distribution and intensity of human activities provides a systematic foundation for ecosystem-based management.

Keywords: anthropogenic impact; coastal and offshore ecosystems; ecological recovery; ecosystem-based management; ecosystem stressor; ecosystem vulnerability; human impact; resilience; threat assessment

Introduction

Conservation and management efforts must prioritize where to spend resources on mitigating impacts of human activities on the environment. This need has become

increasingly apparent in the California Current, a region that stretches roughly from the U.S.-Canada border to central Baja California, Mexico, due to both increasing human population size (and associated environmental impacts) and increased political will and funding for improving ocean management. Recent efforts to address human impacts to the marine ecosystems of this region include the West Coast Governors' Agreement on Ocean Health, California Ocean Protection Council (OPC) and Marine Life Protection Act (MLPA) Initiative, Oregon's Ocean Policy Advisory Council (OPAC), and Washington's Puget Sound Partnership and State Oceans Caucus (SOC) and Ocean Policy Advisory Group.

The process of assessing threats to species and the environment and prioritizing actions to mitigate them has a long history. Many methods have been developed by academics, agencies and conservation NGOs; indeed entire journals and agencies are dedicated to the topic. In the United States, relevant legislation includes the Coastal Zone Management Act, National Environmental Protection Act, Endangered Species Act, Marine Mammal Protection Act, and National Marine Sanctuary Act. All require evaluating the potential negative impacts to species and ecosystems from stressors associated with human activities. Together, these methods have been the focus of thousands of research projects, analyses and reports (e.g., Smit and Spaling 1995, Council on Environmental Quality 1997, Wilcove et al. 1998). Analogous efforts have been conducted by regional and global conservation organizations such as World Wildlife Fund's ecoregional plans (Olson and Dinerstein 1998) and Conservation International's biodiversity hotspots (Myers et al. 2000).

Nonetheless, despite mandates for comparing impacts from multiple stressors, these efforts have largely focused on specific ecosystems, species, or issues. This focus limits their ability to inform the emerging demand for cross-ecosystem, cross-sector comparisons of ecosystem-stressor interactions that are necessary for ecosystem-based management (EBM) (Spaling and Smit 1993, Council on Environmental Quality 1997, U.S. Environmental Protection Agency 1999, Crowder et al. 2006). Indeed, a key challenge for such efforts is that most marine ecosystems are subjected to many different human activities, making it difficult to disentangle the unique contribution and relative importance of each, especially when each ecosystem likely responds differently to the stressors associated with each activity (Halpern et al. 2007). What is needed, then, is a method for assessing vulnerability that is ecosystem-scale and can directly compare across multiple stressors and multiple ecosystems.

Unfortunately, the methods and metrics to quantify ecosystem vulnerability to stressors that have been developed for a single issue, such as pollution, do not provide a means to compare levels of ecosystem vulnerability to stressors across a diversity of issues or ecosystem types. For example, ecotoxicology emerged as a field primarily in order to evaluate how water quality affects species and communities, yet these tools cannot be generalized to other issues. In marine systems, comparative evaluations have tended to focus on particular species (e.g. fish stocks, marine mammals, sea turtles) or issues (e.g., water quality, fishing, habitat loss) where a common currency, such as population size, toxin load, or habitat area

can be used to quantify effects. There are notable exceptions, such as the recent rezoning process on the Great Barrier Reef Marine Park (Fernandes et al. 2005) and The Nature Conservancy and World Wildlife Fund's marine ecoregional assessment processes.

There is growing consensus that ecological vulnerability is a function of exposure, sensitivity, and resilience to stressors (Metzger et al. 2004, Millennium Ecosystem Assessment 2005). This shared framework creates the opportunity to inform and guide EBM through the integration of specific knowledge about vulnerability into an overall assessment of how human activities affect the marine ecosystems within a region. Ideally, assessments of overall vulnerability would be based on empirical data quantifying the expected impact of each stressor on each ecosystem. However, such data are available for only a fraction of the stressor-ecosystem combinations (Halpern et al. 2007).

Because of the lack of comprehensive empirical information on ecosystem-stressor interactions, expert interpretation and synthesis are needed to make existing research directly useful to management. The complexity of these processes is a common challenge in other fields such as engineering, sociology and economics, where expert judgment is often used to predict failure in complex machines (e.g., nuclear power reactors) and understand societies that defy controlled experiments (Morgan and Henrion 1990, Morgan et al. 2000, Fischhoff et al. 2006, O'Hagan et al. 2006). Halpern et al. (2007) presented results from applying a recently developed method for eliciting expert judgments on the vulnerability of marine ecosystems to

anthropogenic stressors. In a quantitative model, experts estimated values of five components of ecosystem vulnerability: spatial scale, frequency, trophic impact, percent change (resistance), and recovery time. The five components, called vulnerability criteria, were based on metrics of exposure and sensitivity to stressors (Table 1). Because ecological vulnerability is a fairly abstract concept, structuring the collection of expert knowledge on vulnerability into these five more concrete factors creates more consistency and transparency to the use of expert opinion. The values for the five criteria are then combined to create a single score, which expresses the relative vulnerability of each ecosystem to each stressor. These quantitative vulnerability scores can be used to rank stressors or rank ecosystems to guide management or conservation priorities in mitigating human impacts. Rather than seeking group consensus, assessments are based on the distributions of expert judgments, allowing users to see the range of opinion.

The Halpern et al. (2007) method has two important shortcomings that are now addressed in this study. First, the five vulnerability criteria were weighted equally when combined into a single score. However, it is possible that experts are more concerned with one criterion, such as recovery time, than another, such as frequency of exposure, when judging what makes an ecosystem vulnerable to a stressor. Although equal weights often approximate more complex weighting schemes (Dawes 1979, Camerer 1981, Dawes et al. 1989), the stakes are high enough in marine resource management to assess weights empirically. Second, experts assessed their uncertainty with verbal quantifiers having no clear quantitative equivalent.

Without a more explicit representation of uncertainty, policy makers cannot know how much faith to place in the judgments, and scientists cannot fairly evaluate their predictions (Morgan and Henrion 1990, O'Hagan et al. 2006, Fischhoff in press).

Our work here takes advantage of a long history in the decision sciences of assessing how to set priorities (e.g., rank threats) when data are scarce and uncertainty exists by using the best available scientific judgments (e.g., Morgan and Henrion 1990, Fischhoff 2005, Willis et al. 2005). Basic research in human judgment has documented many ways in which unaided judgments (e.g. off-the-cuff assessments such as simply listing the rankings of threats) can produce results that do not stand up to more careful validation (Payne et al. 1992, Lichtenstein and Slovic 2006). One common approach to aid the elicitation of expert judgment is to use discrete choice tasks to help experts to summarize their beliefs (Cooke and Goossens 2004). Here we apply one such approach based on ranking hypothetical scenarios of human impact to determine the relative importance of the five vulnerability criteria to expert judgment on how human activities in the California Current affect 19 different marine ecosystems. Variants on this approach have been used to assess risks in other complex, uncertain situations where empirical knowledge is limited, such as complex engineered systems and disaster management (Cooke and Goossens 2004).

In this study we elicited judgments from scientific experts who study marine ecosystems within the California Current region to develop a deeper understanding of marine ecosystem vulnerability to a diversity of anthropogenic stressors. Even in

this data-rich part of the world, critical and numerous gaps in empirical research remain, and our methods help fill these gaps in a low-cost, repeatable, and transparent manner until empirical data are available. Our approach generates a matrix of relative vulnerability scores for every stressor by ecosystem combination that can be useful for management decisions and tools requiring detailed, information about multiple human uses of the oceans at regional scales. Elsewhere we use results from this study to inform a concurrent project mapping human activities across ecosystems in order to identify areas of particularly high or low cumulative impact (Halpern et al. 2009). In addition to informing management efforts dealing with these specific stressors within the California Current, we hope to demonstrate the utility of methods that can be applied elsewhere in the world.

Methods

Generating a matrix of vulnerability scores for all ecosystem-stressor combinations requires three components: 1) a comprehensive list of the relevant ecosystems and human stressors for the region, 2) estimated values for the five vulnerability criteria for every stressor-ecosystem combination, and 3) the weights determining how to combine the criteria values into a single score.

For the first component, ecosystem and stressor lists were based on a previous list (Halpern et al. 2007), refined with input from two experts on California Current ecosystems (personal communication: M. Beck, The Nature Conservancy and M. Ruckelshaus, NOAA Fisheries Service). We included 19 distinct ecosystem types

and 53 anthropogenic stressors. We acknowledge that there are additional historical stressors that humans have not imposed upon the system within the past five years, and some of these stressors have had a lasting effect on the system through to present-day. We ignored these historical stressors and focused only on present-day stressors, which the system has been exposed to within the past five years. To achieve the second and third component, we designed an expert survey focused on estimating the values for the five vulnerability criteria and eliciting their relative importance in judging vulnerability using a discrete choice approach (Appendix A). The five vulnerability criteria were developed previously (Halpern et al. 2007) in a workshop of conservation scientists and ecologists to represent whole-ecosystem vulnerability to a stressor (Table 1; see Appendix A, Part III for more detailed criteria definitions). We use these same five criteria, but with resistance now defined as a continuous variable: percent change. Criteria values take into account both direct effects (e.g. species mortality) and indirect ones (e.g. loss of nursery habitats). The mathematical basis for deriving the vulnerability model and the process of determining the criterion weights using a discrete choice survey are described below.

Multi-criteria decision model

The vulnerability model treats vulnerability as a weighted sum of the five criteria (Table 1) represented mathematically as:

$$\text{Vulnerability(stressor } i\text{, ecosystem } j) = \Sigma_{k=1,..5}\, W_k\, S^{(j)}_{i,\,k}\,, \qquad (1)$$

where $S^{(j)}_{i,k}$ is the value of stressor i on criterion k in ecosystem j and W_k is the weight assigned to criterion k, such that $W_{k \geq 0}$, $\Sigma_{k=1,\ldots 5}\ W_k = 1$. The coefficients, or weights, are normalized so that they sum to unity. The weights are assumed to be the same for all ecosystems and stressors under consideration. This assumption allows for a single model to be applied to all ecosystem-stressor combinations, in turn allowing for direct comparison among them. While many mathematical models exist for combining the weights to create a single value (e.g. linear, logarithmic, polynomial), because environmental vulnerability is expected to be monotonic for all criteria (i.e., higher values denote greater impacts), it can be reasonably approximated by a simple linear model with positive coefficients.

To derive the relative weights W_k of each vulnerability criterion we used a type of discrete choice task in which the expert is presented with a list of hypothetical scenarios of anthropogenic stressors in a specified region and ecosystem type (Table 2; see Part III of the survey instrument in Appendix A). Each scenario represents a different stressor, and hypothetical but realistic values for the five criteria are provided next to each scenario name. The expert must rank the top five scenarios they judge to produce the largest negative human impact at the ecosystem level. The choice of five here is unrelated to the fact that there are five vulnerability factors; it is simply a large enough number to provide necessary data on the expert's decision making process. Ranking the remaining scenarios is not only cognitively challenging but also unnecessary for the statistical analysis (Coombs 1964, Fischhoff 2005,

Lichtenstein and Slovic 2006). The data on the expert's rankings are used in a statistical technique called 'probabilistic inversion' (explained below) to derive the relative weights (summing to one) of the five criteria (Cooke and Goossens 2004, Fischhoff 2005, Du et al. 2006, Neslo 2008; see 'Analyses' section below).

The derivation of the model weights uses a multi-criteria decision model (MCDM), a type of random utility model common to economic theory of utility. The MCDM treats the vulnerability criteria weights as random variables whose joint distribution is chosen to represent a population of experts, from which the elicited experts may be regarded as a random sample. Thus, the confidence intervals on the estimated weights reflect disagreement among the experts. To determine the joint distribution over the weights we used a technique called probabilistic inversion, which inverts a mathematical model at a distribution or set of distributions and is analogous to maximum likelihood estimate methods. Conceptually, the process returns values for the weights that reflect the importance of each weight in the expert's decision making. For instance, if scenarios with large values for recovery time tend to be given high rankings, recovery time would get a large weight, and if trophic impact values show no relationship to the rankings, it would get a small weight.

Operationally and more accurately, probabilistic inversion finds a distribution for a function which maps onto the target distribution for the set of five vulnerability weights. Thus, given potential weights, we may define a function using Eq. (1) which says, in effect, "scenario 20 is ranked first, scenario 7 is ranked second" and so forth.

Our expert elicitation data might in turn indicate, for example, "10% of the experts ranked scenario 20 first, 35% ranked scenario 7 second…" We search for a distribution over the weights which, when pushed through our function, realizes these probabilities. We assume that each expert's ranking is determined by equation (1) but with weights W_k that are specific to that expert. The expert population is represented as a distribution over possible weight vectors (W_1,…W_5). This distribution should be such that, continuing the above example, when sampled a large number of times scenario 7, comes in second place 35% of the time. This correspondence must hold for all scenarios and all rank positions, from first ranked to fifth ranked. Scenarios with both low and high values for each criterion must be included to properly test their relationships to the rankings. Consequently, we chose criteria values for the 30 scenarios to capture the full range of possible combinations. The method used here to search for this distribution is based on the Iterative Proportional fitting algorithm, which finds a constrained maximum likelihood estimate of a joint distribution based on the sorts of constraints discussed above (Csiszar 1975, Kurowicka and Cooke 2006). Analyses were conducted with a program scripted in C+ because no software currently exists for these analyses; one could use other programs separately for the MCDM and probabilistic inversion.

Random utility models allow for internal validation of the model, providing a more explicit and quantitative representation of consensus. Validation is based on: (1) the number of inconsistencies, defined as cases where a hypothetical scenario (ecosystem-stressor combination) with lower scores on all five criteria is ranked as a

greater stressor than a scenario with higher values on all five criteria and (2) the ability of a model built with a subset of the expert discrete choice data to predict the remaining scenario rank orders.

The survey instrument

In May 2007, a preliminary draft of the survey instrument was tested and revised, based on input from a sample group of seven experts, none of whom participated in the final survey. The revised survey (see Appendix A) was then provided to respondents for completion by hand, phone, online, or in-person interview from June to October 2007. We asked experts to focus on one or more of six subregions, delineated to represent jurisdictional and biogeographic regions, and one or more of 19 marine ecosystem types (see Appendix A, Part I). The subregions are Washington, Oregon, northern California (San Francisco and North), central California (South of San Francisco to Point Conception), southern California (South of Point Conception), and Baja California, Mexico (North of Punta Eugenia). Respondents could expand or narrow their focal subregion(s) and ecosystem(s) in different parts of the survey.

The survey had four parts. In Part I, participants provided biographical information, such as professional affiliation(s) (academic, agency, non-governmental organization, or private company), age, and years of scientific experience within each ecosystem and within each geographic subregion. These data were used to test for possible drivers (i.e. bias) of expert judgment. In Part II, participants reviewed the

list of 53 stressors, divided into 22 categories, and ranked the five stressors with the greatest negative impact on their chosen ecosystem and subregion. The 53 stressors were the same on every survey, but the order of the list was randomized by category to minimize potential order biases. Respondents could add or revise stressors. These "stated rankings" were obtained so that we could assess 1) whether we had captured all important stressors and 2) whether the rankings would come out differently when simply stating them directly (i.e., unaided judgments), with no information on vulnerability criteria values and no statistical framework, in comparison to the process of deriving rankings with the MCDM. Part III elicited expert rankings for an individual's top five hypothetical scenarios where criteria values were supplied for example stressors (Table 2), providing the information necessary for the random utility model to derive the weights in Eq. (1). Labels such as "dredging" or "recreational fishing" were provided for the 30 scenarios, even though the values were hypothetical, to provide examples. In order to test the influence of the scenario names on the ranking process, we produced two versions of Part III, one for offshore ecosystems and one for coastal ecosystems, such that eight of the 30 scenarios had different labels but identical criteria values. We used these two expert groups (i.e., offshore and coastal) to compare if weighting values differed by system.

Part IV provided participants with default vulnerability criteria estimates for each stressor affecting their chosen ecosystem, based on values from a global survey (Halpern et al. 2007) or our own judgment (when a stressor was not in the global survey). Stressors not thought to exist or to have no relevant impact in that

ecosystem were assigned 0 for all vulnerability criteria. Participants then used their judgment to accept or revise each estimate, or indicate that they did not know what it should be. These data were used to estimate values for $S^{(j)}_{i,k}$ in the vulnerability model.

Survey respondent pool

For inclusion in the potential respondent pool, we identified scientific experts with personal experience in marine science, conservation, management or policy within the California Current and affiliated with academic institutions, governmental agencies, non-governmental organizations (NGO), or private environmental consulting firms (most scientific experts fall within these four affiliations). Potential respondents were identified via web-based searches using ecosystems, stressors, and location as keywords, based on our knowledge of the field and literature, and by requesting that respondents identify other experts possibly missing from our original list. Invitations were sent to 525 people, including 27 based in organizations located outside of the California Current (in Australia, Canada, mainland Mexico and Baja California Sur, Panama, and Spain). One hundred fifty-five invitees self-identified themselves as non-experts (i.e., inappropriate or mistaken contacts), resulting in 370 potential expert respondents (see Table 3 for expert attributes). An additional 130 of these never responded so it is unclear whether they received the invitation or were truly appropriate experts, leaving a pool of 240 confirmed potential experts.

Analyses

Producing vulnerability criteria weights

Prior to all analyses, scale and frequency measures were transformed (i.e., scale = ln[scale*100] and frequency = ln[frequency*360]) to produce positive values on roughly equivalent scales as the other three criteria. This rescaling helps avoid a single criterion driving results simply because it has higher values from which to choose. For each hypothetical scenario in Part III, we calculated the percentage of experts who ranked the scenario first, second, third, fourth, and fifth and then used probabilistic inversion to calculate the weights that best reproduced these observed percentages. Results were compared for model runs using the first ranking, the first two rankings, the first three, and the first four ranks in order to evaluate if number of ranks used affected the weighting values. We calculated these weights for all respondents (N = 102; five experts did not fill out this part of the survey) and for coastal (N = 66) and offshore (N = 36) versions of the survey to evaluate if system (coastal vs. offshore) affected weight values.

To test the validity of our multidimensional vulnerability model we first assessed the degree to which our five vulnerability criteria capture what factors experts use to rank vulnerability. To do this we compared the number of inconsistencies in scenario rankings (e.g., a case where a scenario with high values for all vulnerability criteria and one with low values are both ranked highly) with the number of inconsistencies generated by a null hypothesis that experts rank scenarios randomly without regard for the criteria values. If more inconsistencies emerge than would be

expected at random, either experts used criteria beyond the five provided and/or experts did not understand or correctly execute the task. This method is one way to quantify the degree of consensus in expert judgment using a measure of internal validity. We also used criteria weights from the model based on the first four ranked scenarios to predict experts' fifth-ranked scenario and compared these to actual fifth ranks from expert judgment to assess how well our model captured expert judgment.

Ecosystem vulnerability scores

Vulnerability criteria values from Part IV were averaged across replicates (i.e., surveys completed by participants) for each ecosystem to estimate $S^{(j)}_{i,k}$ and combined with the weights W_k in (Eq. 1) to produce a vulnerability score for each stressor-by-ecosystem combination. We also calculated an overall average score for each stressor from the average scores for the 19 ecosystems and an average ecosystem vulnerability score from the scores for the 53 stressors for each ecosystem and used these averages to compare among subregions and between coastal and offshore ecosystems. We were unable to rigorously test whether ecosystem vulnerability scores differed by subregion because this test requires the sample size for an ecosystem to be large in all six subregions and in no case did this occur. However, sample size was large enough for 17 ecosystem-subregion comparisons (see Table 4 for specific pairwise comparisons) to allow for a partial test of subregional differences. To compare vulnerability scores between subregions for a given ecosystem we (1) averaged stressor vulnerability scores across respondents

within a single subregion (instead of lumping subregions), (2) used two-tailed paired-sample t-tests to test for significant differences across subregions, and (3) used correlations to measure the strength of simple linear relationships between ranking values for sub-regions for the full set of stressors. Stressors were excluded from individual surveys when one or more of the vulnerability criteria were not provided or when a subregion had only a single response for the stressor (e.g., some respondents did not fill in values for all 53 stressors).

Potential respondent bias

We used chi-square tests to evaluate potential differences between responders and non-responders based on gender or affiliation. Within the responder group, we examined possible differences in experts' assessment of criteria values (Part IV) based on demographic information collected in Part I, using ANOVA (for affiliation), t-test (for gender), and least squares regression (for years of experience). For these tests we averaged all criteria values from all stressors, transformed as described above, for each respondent. Seven experts did not complete this section, resulting in a sample size of 95.

Comparing directly stated and modeled ranks

We also compared experts' directly stated ranks, collected in Part II, to the ranks produced by the model using Spearman's rank correlation analysis. Because ecological vulnerability to stressors is a fairly abstract concept, we expected little

consistency in top rankings from Part II across experts, and substantial deviation of these rankings from those generated by the statistical model, which breaks down the abstract concept into more concrete, specific subcomponents that are each quantified separately. To rank directly stated responses, we counted how often each stressor was among experts' top five ranks regardless of ecosystem. This method was chosen over a strict average rank because it is less sensitive to unusual high rankings. We used average ranks to break ties.

Results

Survey pool

Out of the 240 confirmed potential expert respondents, 107 responded (45% response rate) by completing one or more surveys (N = 160 surveys). Respondents were from academic institutions (52%), government agencies (31%), NGOs (15%), and private consultants (2%) and included 80 males (75%) and 27 females (25%) (Table 3). Thirty-nine respondents (36%) filled out more than one survey, 49 surveys addressed more than one subregion (average = 1.6 subregions ± 0.1 SE; maximum = 6), and 9 surveys addressed more than one ecosystem (average = 1.1 ecosystems ± 0.1 SE; maximum = 9). One survey was eliminated due to unclear responses. The completed surveys covered 95 of the 120 possible ecosystem-by-subregion combinations, with one to 13 surveys per combination (see Appendix B). As no expert evaluated vents/seeps, this ecosystem was excluded from all analyses. Respondents' maximum reported years of experience within the marine ecosystems

or subregions averaged 18.6 yrs ± 1.1 SE. On average respondents had 14.4 years of experience ± 0.9 SE within their chosen ecosystem and 13.9 years of experience ± 0.6 SE within their chosen subregion (see Appendix C for average years of experience per ecosystem per subregion). Additionally, offshore ecosystems tended to be evaluated by fewer experts (3.2 ± 1.0 SE) than coastal ecosystems (7.2 ± 1.4 SE). Of the 263 potential respondents who did not complete a survey, 130 never responded (after at least three reminders), 115 did not respond after initially accepting the invitation (and after at least three reminders), 12 declined but gave no reason, and six declined because they did not feel comfortable filling out the survey.

Potential survey bias

Affiliation and gender did not significantly differ between invited experts who completed the survey (responders) and those who did not (non-responders) (affiliation: $\chi^2 = 6.75$, df = 3, $P = 0.08$, gender: $\chi^2 = 0.121$, df = 1, $P = 0.728$; Table 3). The marginal significance for affiliation is due to the higher rate of response from academic experts. Vulnerability criteria values $S^{(j)}_{i,k}$ (Part IV) showed no significant differences associated with affiliation (ANOVA: $F_{3,93} = 0.36$; $P = 0.78$), gender (t-test: t = 1.86; $P = 0.07$), or years of experience (bivariate linear regression: $R^2 = 0$; $P = 0.88$). The marginally significant result for gender reflected a single extreme outlier; when removed, gender showed no trend (t-test: t = -0.058; $P = 0.95$).

Vulnerability criteria weights and model validation

The MCDM produced highly uneven weightings for the five vulnerability criteria. Percent change in biomass (resistance) and trophic impact together explained 89% of the overall weights of ecosystem vulnerability (66.5% and 22.1%, respectively). Recovery time had a small contribution to the overall vulnerability score (Table 5). These weights were highly consistent regardless of the number of ranks used to develop the model (one, two, three, or four). Using the top four ranks produced good predictions of the stressor ranked fifth by the experts; the frequency of each scenario being predicted to be fifth was highly similar to the frequency of experts selecting it as their fifth-ranked scenario (mean difference 0.001 ± 0.01 SE). Furthermore, there were significantly fewer inconsistencies than expected by random. Twenty-three of the 30 scenarios could produce inconsistencies, i.e. ranking one of these scenarios higher than the other seven would be 'inconsistent,' and of the 102 experts only 15 chose one of these inconsistent scenarios as rank 1. The probability of observing so few inconsistencies is extraordinarily low (7×10^{-40}), suggesting that experts generally understood the ranking task.

Vulnerability scores

Vulnerability scores for all ecosystem-stressor combinations are provided in Table 6. Sample sizes for the criteria values used to produce these scores ranged from 0 to 17. Across all values experts assigned to the five criteria, 25.5% were marked zero (i.e., stressor was not a threat to the ecosystem), 21.0% marked "don't know," 12.9% left blank, and 0.3% marked "disagree" (i.e., experts disagreed but did

not provide an alternate value). If a stressor-ecosystem combination had no expert responses, we used default criteria values from previous analyses (Halpern et al. 2007). There is a significant relationship between average sample size and average vulnerability score per ecosystem (linear regression: $R^2 = 0.30$, $P = 0.02$), suggesting that low response rates for some ecosystems may have resulted in lower vulnerability scores. However this relationship has a low R^2 and is not significant when ecosystems with an average sample size of less than four (Table 6) are excluded ($R^2 = 0.02$, $P = 0.76$). Stressors were evaluated by 88.9 ± 0.6 SE experts on average.

Ocean acidification in soft slope, hard slope, and in hard deep ecosystems had the highest vulnerability score observed (3.4) and scores for this stressor exceeded 1.2 for all ecosystems (Table 6). On average, scores were greater in coastal than offshore ecosystems, most notably higher (>1.0 difference) for sea level rise, UV change, altered flow dynamics, habitat alteration, and invasive species. Only demersal destructive fishing was notably higher in offshore ecosystems. Coastal ecosystems were judged most vulnerable to (in decreasing order) invasive species, ocean acidification, sea temperature change, sea level rise, and habitat alteration from coastal engineering, while the stressors with the highest scores for offshore ecosystems were (in decreasing order) ocean acidification, demersal destructive fishing, shipwrecks, military activity, and lost fishing gear (Table 6). On average, coastal ecosystems were judged to have some degree of vulnerability (scores > 0.0) to nearly all of the 53 stressors evaluated here (43.7 stressors ± 2.2 SE), while

offshore ecosystems were estimated to be vulnerable to less than half of the stressors (24.6 ± 3.7 SE).

There were over 30 additional stressors that experts felt were not appropriately captured by our 53 stressors (see Appendix D). Some of these include: alteration of tributaries and watersheds, altered oceanographic regimes (e.g., wind, circulation, or upwelling) due to climate change, global temperature change (not just sea temperature change), non-toxic algal blooms, illegal harvesting (poaching or harvesting by public), kelp harvesting, wave energy development, and oil exploration and drilling (as distinguished from oil rigs and ocean mining).

Subregional comparisons

Overall, the four middle subregions (Oregon and the 3 California subregions) had no significant differences in vulnerability scores for the ecosystems for which comparisons could be made, except for the central California and Oregon rocky reef ecosystem comparison (Table 4). For the one ecosystem for which comparisons could be made to Washington (rocky intertidal), the Washington subregion differed significantly from all other subregions except central California but had highly correlated values in all of these cases ($R^2 > 0.72$). Baja California was significantly different from northern and southern California in vulnerability scores for seagrass ecosystems (as well as Washington in rocky intertidal ecosystems) and also had low correlation values. Vulnerability scores for rocky intertidal ecosystems in Baja did not differ significantly from central and southern California.

Comparing directly stated and modeled ranks

Spearman's rank correlation between directly stated ranks (Part II) and model-derived average vulnerability scores (average values across ecosystems from Part IV) is significant ($P = 0.001$) but relatively low ($\rho = 0.44$). The five most commonly directly stated top five stressors were sea temperature change (42% of respondents ranked it in their top five), recreational fishing (33%), habitat alteration from coastal engineering (32%), increasing sediment loads (22%), and invasive species (22%), yet of these only sea temperature change and invasive species were among the top five modeled vulnerability ranks (Table 7) and recreational fishing and sediment increase were not among the top 10 modeled ranks. Ocean acidification received the highest modeled vulnerability score, yet was included in only 11% of respondents' stated top five stressors. Additionally, UV change, sea level rise, benthic structures, shipwrecks, and hypoxic zones caused by nutrient input were only included in ≤ 7% of stated top five stressors, yet all appeared among the top 10 modeled ranks. Remarkably, all but three of the 53 stressors were ranked by at least one expert in their top-five stated stressors (across all ecosystems).

Discussion

Decision theory approach to assessing ecosystem vulnerability

Our approach moves beyond previous methods for assessing environmental risk in several key ways. The decision rules (criteria) and relative importance of those

criteria (weights) are explicit and quantified, rather than implicit and qualitative as is the case for most Delphi processes. The structured approach to assessing these criteria and weights compels experts to take an ecosystem-level perspective when evaluating the importance of stressors and explicitly consider (and quantify) exposure and sensitivity aspects of vulnerability, rather than, for example, focusing only on a single species within the ecosystem they study. Vulnerability is an abstract concept and defining it at an ecosystem-level scale adds further complexity to the concept. This complexity challenges an individual's cognitive ability to compare the vulnerability of ecosystems to various stressors in a consistent and fair manner without the aid of a model built from concrete subcomponents. Indeed, experts' directly stated top stressors showed little correlation with the modeled top stressors. When experts simply list key stressors, there is no way to know why they chose those stressors, with responses potentially subject to biases that cannot be tested (Payne et al. 1992, Slovic and Lichtenstein 2006). Using a mathematical model, however, requires knowing which subcomponents to use in building the model and how to combine subcomponents in a way that matches expert's decision-making process. The subcomponents (i.e. vulnerability criteria) come from a long history of research on the topic; the MCDM fills the latter role of combining subcomponents. The MCDM revealed that experts primarily used percent change (i.e. resistance) and trophic impact when evaluating ecosystem vulnerability to stressors, despite that vulnerability is thought to also be a function of exposure, not just measures of sensitivity (Metzger et al. 2004, Millennium Ecosystem Assessment 2005).

The MCDM also allowed us to test how consistently experts used the vulnerability criteria in their assessments (i.e., internal model validity) by comparing results from two versions of the survey based on different systems (coastal vs. offshore), calculating model weights using different numbers of scenario rankings, and using the model to predict the next-ranked stressor. These comparisons do not allow us to test the uncertainty of individual experts but do provide several methods for testing and quantifying variability (i.e. degree of consensus) among experts, a key improvement over our previous approach (Halpern et al. 2007). We found high model validity in all cases: model weights were consistent between systems and with different numbers of ranks used to build the model, and the ecosystem vulnerability model predicted well the next-ranked stressor. This ability to evaluate model validity is rare among methods for eliciting expert judgment. The robustness of the model suggests that the vulnerability model can be used with the same values for the criteria weights to evaluate new stressors and ecosystems not included here. Thus, the model provides a rapid way to consider expert opinions on additional and emerging ocean uses, such as wind and wave farms or liquefied natural gas (LNG) terminals, and quickly 'slide' them into the appropriate rank order once their vulnerability scores are estimated. However, especially with new ocean uses, these opinions cannot replace actual empirical data on ecological effects, but they can be used to direct research to assess potential ecological impacts.

The vulnerability model solves the 'apples to oranges' problem of making comparisons between very different types of systems, and the use of expert judgment

allows filling knowledge gaps temporarily until empirical data is generated or improved. The vulnerability model, in particular, differentiates our work from other efforts to rank stressors to ecosystems (Olson and Dinerstein 1998, Myers et al. 2000, Pew Oceans Commission 2003, Metzger et al. 2004, Millennium Ecosystem Assessment 2005). In this structured framework, judgment is a means to incorporate knowledge efficiently and understand the world. We do not suggest that expert judgment is a replacement for empirical data. The approach presented here benefits from greater transparency and repeatability than most other expert judgment elicitation procedures.

Ecosystem vulnerability in the California Current

Ecosystem-based approaches to resource management require knowledge of how each ecosystem responds to the stressors associated with human uses of the ocean, yet empirical information on such responses is limited. Using a decision theory method for eliciting expert judgments, we have evaluated the vulnerability of 19 marine ecosystems within the California Current region to 53 different stressors, a total of 1007 stressor-by-ecosystem combinations. There are both expected and unanticipated aspects to the vulnerability assessments for the California Current. Averaged across all ecosystems, stressors with high vulnerability scores were associated with climate change, invasive species, habitat destruction (benthic structures, coastal engineering), and pollution, all of which have been previously highlighted as key issues (Vitousek et al. 1997). Coastal ecosystems were assessed

to be more vulnerable to human stressors, and to a higher number of stressors, than offshore systems. At the ecosystem level, rank order of stressors by vulnerability scores varies greatly with ecosystem type, as is expected. More unexpectedly, ocean acidification topped the rankings for many ecosystems. This result highlights the urgent need to develop strategies for addressing this climate stressor. However, very few experts listed ocean acidification, UV change, and sea level rise among their top five stated ranks, yet these all fell within the top 10 modeled ranks. This inconsistency between the two methods of ranking highlights the need for greater awareness of these climate stressors; experts agree that these stressors rank highly based on the vulnerability criteria, however, it did not occur to experts to rank these stressors highly in the stated-rank exercise. On the other hand, sea temperature change and invasive species ranked high for both ranking methods, thus experts categorize these stressors as high based on the vulnerability criteria and are aware of the importance of these stressors without necessarily considering the vulnerability criteria. Modeled results ranked commercial fishing as a top stressor in most offshore ecosystems (Tables 6, 7), as has been found by many others (e.g., Pauly et al. 1998, Myers and Worm 2003, Worm et al. 2006), but across all ecosystems the five types of commercial fishing showed lower vulnerability scores than many other stressors. This is because experts judged pelagic fishing to have very little or no impact on many ecosystems and land-based sources of stress to have larger impacts on a suite of coastal ecosystems. Fishing may have ranked lower as well because our

approach focuses on present-day stressors and therefore ignores the historical, accumulated stress of fishing (in particular overfishing) on ecosystems.

Although many of these expert opinions on the top stressors or most vulnerable systems may seem expected or known, it is extremely valuable to test these expert opinions with a rigorous scientific approach and assess the level of consensus on rankings among experts. Results from a rigorous survey can provide support to management decisions, and although decisions should ultimately be made based on scientific evidence, the value of the supporting role of expert opinion should not be underestimated given the politically-charged environment in which these decisions are often made.

Although these relative stressor rankings are valuable for aiding conservation and management prioritization efforts, another useful result is the matrix of quantitative vulnerability scores that is produced (Table 6). These scores not only give a quantitative, relative estimate of vulnerability of an ecosystem to each stressor (e.g., kelp forests are judged to be five times as vulnerable to ocean acidification as they are to shellfish aquaculture) but also allow direct and quantitative comparisons of stressor vulnerability among ecosystem types (e.g. rocky reefs are judged to be 30% more vulnerable to recreational fishing than seagrass beds are to organic pollution). This ability to compare very different entities in a quantitative manner has broad potential application and relevance to various cost-benefit analyses of how and where to prioritize management, mitigation, and conservation effort.

A key challenge for any effort to evaluate cross-ecosystem, cross-sector vulnerability is to decide how much to lump or split categories of stressors and ecosystems. Fishing can be considered as a single stressor, as five categories of stress (as we have done here), or as many categories in which each species and gear type is evaluated separately. Similarly, habitats can be classified according to any number of physical and biological attributes (e.g., sediment grain size or type, tidal flux, depth, relief, wave exposure, upwelling characteristics, temperature, salinity, species composition and diversity) (Carlton 2007), which can lead to few or many habitat types depending on these decisions. For example, one could choose to lump all salt marshes together as a single ecosystem type or split them into estuarine and coastal salt marshes. Here we strove to focus on a level of habitat classification that was general enough to likely be addressed by management efforts in the California Current but fine enough to capture important differences, and a level of stressor classification that captures important differences in potential impact to ecosystems from subdivisions of a stressor class but is general enough to match typical management focus. Additionally, we have assumed that experts take into account the temporal dynamics of oceanographic and climatic processes (e.g., El Niño Southern Oscillation cycle, the Metonic cycle, the Pacific decadal oscillation (Halpin et al. 2004)) when assessing the influence of a particular stressor on an ecosystem. However, our survey focused on assessing the present-day (within the past five years), so longer temporal dynamics could be the focus of future studies. In summary, our method for assessing ecosystem vulnerability can easily be adapted to

assess a different classification scheme, spatial scale/extent, or time period and directly compared to our output here.

Our assessment of the differential vulnerability of ecosystems does not account for potential synergistic effects among stressors, where some combinations of stressors may lead to greater impacts than our estimates here, resulting in higher scores. These synergisms are currently poorly understood (Crain et al. 2008, Darling and Cote 2008), so it is difficult to account for them in the vulnerability model. Also, the default vulnerability criteria values provided in Part IV may have influenced experts, or experts may have been reluctant to modify defaulted values unless they felt them to be radically wrong. An alternative would have been to leave these values blank, but experts tend to skip blank values (Halpern et al. 2007).

Ultimately the accuracy of the vulnerability scores depends on the quality of expert judgment. We were careful to include only experts with empirical knowledge and experience in marine ecosystems within the California Current but recognize that this does not ensure accuracy. In order to attempt to quantify reliability of expert judgment and examine the basis upon which experts form their opinions, future studies could assess (1) whether vulnerability estimates were based on actual data, (2) if vulnerability estimates were based on actual data, the spatial extent of these data, (3) if experts had peer-reviewed research published within the field of study evaluated (both stressor and ecosystem combination), and (4) the degree of confidence in each vulnerability estimate. However, we recognize that there is no way to objectively quantify the degree of accuracy of expert opinion before empirical

data exist. Carefully controlled experiments that clearly show the relative vulnerabilities of ecosystems to different stressors are the gold standard for environmental risk assessment. When these data are available for a particular region or set of stressors, they should be compared to the expert opinions to examine the degree of accuracy. The day is far off when such data exist for the numerous ecosystem-stressor combinations, so perhaps researchers should prioritize gathering these data before relying solely on expert opinion for any management decisions. Until then expert judgment elicitation can provide some guidance to management efforts, and our methods offer a quantitative alternative to setting priorities based on a simple task of ranking threats.

Management implications

Our approach and results can be used in a number of ways to inform and aid management efforts and particularly address the fundamental question of how and where to prioritize stressor and ecosystem management. Our results alone cannot answer that question, as there are many dimensions (socio-economic, opportunities, etc.) that drive such decisions, but our quantitative vulnerability scores can provide a key piece of the answer. The matrix of vulnerability scores based on expert judgment informs which stressors are likely most important to address, which ecosystems are likely most vulnerable, and which factors (i.e. criteria) likely drive that vulnerability. Even if these results are believed to be known, having a quantitative and transparent

method for assessing vulnerability is of enormous value to anyone or any organization that must explain and defend their management decisions.

Our analyses provide results most appropriate for state- and federal-level management or conservation organizations focused on large biogeographic regions or the California Current as a planning unit. At this scale, the high vulnerability scores of most ecosystems for climate change stressors point to the immediate need for local, state, federal, and international action to address this key stressor for nearly all ecosystems. Two of the high-scoring stressors revealed by our analysis, invasive species and coastal engineering, highlight management challenges that might be most successfully addressed at different spatial scales. Although removal of existing invasive species may be possible by local action, it is generally very difficult, and the risk of new species invasions can only be reduced by state, federal, and even international regulations that control the movement of species (i.e., vectors such as ballast water, hull fouling, aquaculture, and aquarium trade) (Bax et al. 2001, Ruiz and Carlton 2003). Given the difficulty of eradicating invasive species and reversing their impacts on local ecological communities, prioritizing the reduction of invasive species risks at the regional level may have a high ecosystem-wide payoff. Habitat alteration due to coastal engineering also had high scores in several coastal ecosystems. Although it is difficult to reverse fully, it can be regulated and managed locally at the scale at which it occurs, and there are some options for local habitat restoration. For local-scale management, vulnerability rankings could be different. Fortunately, our framework is fully scalable, with the model weights expected to be

consistent across scales and locations, and the output allows for quantitative, relative vulnerability assessments that are often not intuitive or known. The model also provides a rapid method for assessing the potential impact of new stressors relative to existing stressors, and in theory the same stressors in new locations where one would simply need to gather new criteria scores (Part IV of the survey).

These results provide a critical piece of information for moving towards marine ecosystem-based management (EBM) and ocean zoning, but they are clearly not all that is needed for effective management. Among other things, EBM requires consideration of spatial patterns of cumulative impacts of human activities on ecosystems (McLeod et al. 2005, Halpern et al. 2008a), and in order to map cumulative impacts, one needs information on the relative vulnerability of ecosystems to those stressors, as presented here, along with information on the intensity of each stressor (Crowder et al. 2006, Halpern et al. 2008b, Halpern et al. 2009). Such mapping also allows one to assess the realized impact of each stressor on each ecosystem, rather than the expected vulnerability as is captured here. Ultimately, effective management and conservation also require assessments of the costs and benefits of any management action, recognition of logistical and financial constraints, compromises for political feasibility, and the flexibility to manage adaptively as new information becomes available. Without knowledge of relative ecosystem vulnerability to different human activities, however, ecosystem-based management will be difficult if not impossible to achieve.

Acknowledgements

We are very grateful to the 107 experts who participated in the survey and the seven participants in the pre-survey. We thank J. T. Carlton and S. D. Gaines for their valuable comments on an earlier version of this manuscript. This work was generously supported by a grant from the Gordon and Betty Moore Foundation (to B. S. Halpern, K. A. Selkoe, C. V. Kappel, C. M. Crain, and F. Micheli) and the National Center for Ecological Analysis and Synthesis (B. S. Halpern, K. A., Selkoe, and C. V. Kappel).

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Tables

Table 1. Description of the five vulnerability criteria used to evaluate ecosystem vulnerability to each stressor.

Vulnerability criterion	Description
Spatial scale	The spatial scale (km^2) at which a single act of an activity impacts the ecosystem, both directly and indirectly.
Frequency	The mean annual frequency (days per year) of the activity at a particular location within a given region.
Trophic impact	The primary extent of marine life affected by an activity within a given ecosystem and region.
Percentage change	The degree to which the species, trophic level(s), or entire ecosystem's "natural" state is impacted by the activity.
Recovery time	The mean time (in years) required for the affected species, trophic level(s), or entire community to return to its former, "natural" state following disturbance by a particular activity.

Table 2. In Part III of the survey, each respondent received either a coastal or offshore version of the table below with 30 hypothetical scenarios (only a subset is presented here). All criteria values were identical between the coastal and offshore versions, but some scenario names were different.

Coastal	Offshore	Spatial extent (km^2)	Frequency (no./yr)†	Trophic impact (level 1–4)	Percentage change	Recovery time (yr)
Aquaculture: marine plant	Aquaculture: finfish (predators)	2	360	1	20	1
Aquaculture: shellfish	Shipping: commercial, cruise, ferry	5	360	1	5	0.1
Climate change: sea level rise		10 000	1/2	2	20	5
Climate change: sea temperature change		50 000	1	3	25	50
Climate change: UV change		10 000	1/10	1	5	1
Coastal engineering: habitat alteration	Ocean mining: sand, minerals, etc.	1	1	4	75	25
Direct human impact: trampling	Disease/pathogens	150	360	2	35	25
Fishing: demersal destructive		8	1/20	4	10	0.5
Fishing: demersal nondestructive low bycatch		0.1	1/20	1	10	0.5
Fishing: nondestructive artisanal‡	Fishing: demersal nondestructive high bycatch	1	1/20	1	50	1

Notes: Survey respondents were asked to rank the five hypothetical scenarios with the greatest impact based upon the vulnerability measures provided in the table. Respondents were also asked to not limit their ranking to a particular region and ecosystem, in contrast to the "stated ranks" activity, because the numbers represent a hypothetical coastal or offshore ecosystem in a hypothetical region.

† Fractions such as 1/2, 1/10, and 1/20 signify once every 2, 10, and 20 years.

‡ Artisanal refers to fishing practices such as traditional fishing on a small-scale, often subsistence or small-scale commercial fishing.

Table 3. Number of survey responders and nonresponders per affiliation and gender category.

	Affiliation				Gender		
Category	Academic	Agency	NGO	Private	Male	Female	Total
Nonresponders	120	94	49	0	192	71	263
Responders	56	33	16	2	80	27	107
Total	176	127	65	2	272	98	370

Table 4. Subregional comparisons of four ecosystems (kelp forest, rocky intertidal, rocky reef, and seagrass) based on linear correlations of all stressor values and two-tailed paired-sample t tests.

Ecosystem and subregional comparison	*N*	Correlation	*t*	*P*
Kelp forest				
CCA vs. SCA	49	0.60	−1.05	0.30
Rocky intertidal				
WA vs. OR	33	0.90	7.30	<0.0001
WA vs. CCA	23	0.72	1.94	0.07
WA vs. SCA	45	0.87	5.02	<0.0001
WA vs. BCA	27	0.86	5.57	<0.0001
OR vs. CCA	20	0.75	1.39	0.18
OR vs. SCA	33	0.93	−1.98	0.06
OR vs. BCA	23	0.95	0.03	0.98
CCA vs. SCA	24	0.75	−1.78	0.09
CCA vs. BCA	14	0.62	−0.93	0.37
SCA vs. BCA	29	0.89	−1.19	0.25
Rocky reef				
OR vs. CCA	8	0.79	−2.75	0.03
OR vs. SCA	17	0.71	−1.02	0.32
CCA vs. SCA	4	0.96	−0.18	0.87
Seagrass				
NCA vs. SCA	19	0.77	2.03	0.06
NCA vs. BCA	14	0.36	−3.03	0.01
SCA vs. BCA	39	0.35	−5.18	<0.0001

Notes: Sample sizes (*N*), correlation coefficients, *t* ratios, and *P* values are shown. Abbreviations for subregions: WA (Washington), OR (Oregon), NCA (northern California), CCA (central California), SCA (southern California), and BCA (Baja California, Mexico).

Table 5. Mean weighting values for vulnerability criteria based on model results from the first stressor, and the first two, three, and four stressors ranked.

Model	No. top ranks included	Spatial extent (km^2)	Frequency (no./yr)	Trophic impact (level 1–4)	Change (%)	Recovery time (yr)
Combined	1	0.033	0.053	0.201	0.692	0.020
	2	0.067	0.089	0.299	0.532	0.014
	3	0.073	0.044	0.198	0.672	0.014
	4†	0.061 ± 0.008	0.046 ± 0.007	0.221 ± 0.022	0.665 ± 0.029	0.008 ± 0.001
Coastal	4	0.072	0.046	0.226	0.650	0.006
Offshore	4	0.055	0.057	0.250	0.624	0.015

Notes: All surveys were included in the "combined" models; results of separate model runs for "offshore" or "coastal" ecosystem surveys are shown only for the first four stressors ranked. The second column gives the number of top stressor ranks used to calculate the model. Standard error (±SE) is given for the combined model using the first four stressors ranked.

† Model used for subsequent analyses.

Table 6. Vulnerability scores for 53 stressors in 19 ecosystems.

Stressors	Coastal ecosystems									Offshore ecosystems			
	KF	RR	SG	Shl	SR	BE	MF	RI	SM	SSh	SSl	SD	HSh
Aquaculture: finfish (herbivores)	0	0	0	0	0	0	0	0	0	0	0	0	0
Aquaculture: finfish (predators)	0.2	1.0	0.3	0	0	0	0	0.2	0	0.9	0.5	0	0.7
Aquaculture: marine plant	0	0	0.4	0	0	0	0.3	0.8	0.4	0	0	0	0
Aquaculture: shellfish	0.4	0.5	1.6	0.5	1.5	0	1.1	1.0	0.9	0.2	0	0	0
Benthic structures (e.g., oil rigs)	1.6	1.7	1.6	1.4	2.0	1.4	2.4	0.9	1.8	2.2	1.4	0.4	2.4
Climate change: ocean acidific.	2.0	2.2	2.1	1.2	2.5	1.8	2.4	3.1	2.4	2.6	3.4	2.5	2.7
Climate change: sea level rise	1.8	1.5	1.9	0	2.2	1.7	1.9	2.7	2.5	0	0	0	0
Climate change: sea temp. change	2.9	2.2	1.9	0	2.2	1.7	1.8	2.7	1.8	1.7	0.6	0.5	1.9
Climate change: UV change	1.6	1.7	1.5	0	1.8	1.8	1.7	2.3	1.9	0	0	0	0
Coastal engineer.: alt. flow dynam.	1.2	0.7	1.1	0.6	2.4	1.3	2.0	1.5	2.5	0.2	0	0	0
Coastal engineer.: habitat alteration	1.4	1.1	1.6	0.6	2.4	1.3	2.1	1.7	2.7	0.2	0	0	0
Direct human impact: trampling	0.1	0.2	0.8	0.3	0	1.7	0.3	1.6	1.0	0.1	0	0	0
Disease/pathogens	1.0	1.0	0.9	0	1.5	1.1	1.1	1.1	0.8	0.9	0	0	1.1
Dredging	0.1	0.2	1.7	0.5	2.2	1.6	1.7	0.2	1.3	0.6	0	0	0
Fishing: aquarium	0.7	0.7	0.1	0	0	0	0.1	0.6	0.1	0.2	0	0	0
Fishing: demersal destructive	0.3	1.2	0.2	1.2	0	0.9	1.1	0.7	0.3	2.0	2.3	2.2	1.6
Fishing: demrs. non-des. high byc.	1.2	1.3	0.6	0.6	0.8	1.3	0.9	0.4	1.0	1.3	1.3	1.3	1.3
Fishing: demrs. non-des. low byc.	1.2	1.2	0.5	0.4	1.6	0.8	0.7	0.4	0.8	0.8	0.9	0.8	1.1
Fishing: destructive artisanal	0.2	0.1	0.2	0	1.5	0.8	0	0.7	0.8	0	0	0	0
Fishing: non-destructive artisanal	0.2	0.3	0.4	0.2	0.9	0.7	0.6	0.8	0.6	0.2	0	0	0
Fishing: pelagic high bycatch	0.3	0.9	0	0	0	0	0	0.2	0.6	0.2	0	0.1	0
Fishing: pelagic low bycatch	0.2	0.8	0	0	0	0	0	0	0.4	0.3	0.3	0	0
Fishing: recreational	1.5	1.4	0.9	0.8	0.9	1.0	1.1	1.2	1.0	0.4	0	0.8	1.2
Freshwater input: decrease	0.2	0.1	0.6	0	0	0.6	1.1	0.8	1.5	0	0	0	0
Freshwater input: increase	0.8	1.0	0.8	0	0.8	0.9	1.2	1.1	1.4	0	0	0	0.8
Invasive species	2.4	1.8	1.7	1.3	2.1	3.2	3.0	2.6	2.0	0.7	0	1.1	1.5
Marine component of forestry	0	0	0.5	0	1.1	0.6	0.7	0.5	0.9	0.3	0	0	0
Military activity	1.0	0.3	0.8	0.6	0	1.4	0.8	0.4	0	1.3	1.2	1.2	1.3
Nutrient input: causing HABs	1.1	1.3	1.1	0.5	2.1	1.7	1.7	1.1	1.4	1.1	0	0	1.4
Nutrient input: causing hyp. zones	1.0	1.2	0.9	0.4	2.2	1.5	1.6	0.8	1.4	1.5	0	0	1.8
Nutrient input: into eutrophic water	0.9	1.0	0.9	0.3	2.2	1.5	1.0	0.9	0.9	1.0	0	0	1.2
Nutrient input: into meso. water	1.2	0.9	0.9	0.3	2.2	1.1	1.2	1.0	1.5	0.8	0	0	1.3
Ocean dumping: lost fishing gear	1.1	1.1	0.9	0.4	0.5	1.5	1.4	1.0	1.2	1.2	1.3	1.2	1.2
Ocean dumping: marine debris	0.8	0.9	0.6	0.4	0.6	1.0	1.0	0.9	1.0	0.8	0.9	0.8	1.0
Ocean dumping: ship wrecks	1.7	2.1	1.5	1.0	2.3	1.6	2.3	1.5	0	1.8	1.6	1.3	2.4
Ocean dumping: toxic materials	0.9	1.0	1.1	0.5	1.7	1.4	1.5	0.9	1.4	1.1	1.1	1.1	1.1
Ocean mining (sand, minerals, etc.)	0.1	0	0.5	0	0	1.1	0	0.1	0	1.3	1.6	0	0
Ocean pollution (from ships/ports)	0.9	1.0	0.9	0.4	0	0.8	1.3	1.3	1.1	0.8	0	0	1.0
Pollution input: atmospheric	1.0	1.1	1.0	0	1.3	0.9	1.3	1.1	1.4	1.1	0	0	1.2
Pollution input: inorganic	1.3	1.5	0.9	0.8	1.4	1.3	1.3	1.2	1.4	1.6	2.0	1.9	1.1
Pollution input: light/noise	0.1	0	0.6	0.3	1.3	1.2	1.2	0.9	1.2	0.2	0	0	0
Pollution input: organic	1.3	1.5	1.1	1.4	1.5	1.9	1.9	1.3	1.4	1.5	2.0	2.5	1.3
Pollution input: trash, urban runoff	0.7	1.2	0.9	1.0	1.0	1.2	1.2	1.1	1.1	0.9	1.2	1.9	0.4
Power, desalination plants	0.8	1.1	0.5	0.5	0	1.7	1.3	1.5	1.2	0.2	0	0	0
Scientific research: collecting	0.7	0.7	0.6	0.1	0	0.7	0.7	0.8	0.9	0.9	1.3	0.7	0.7
Scientific research: expts./surveys	0.7	0.8	0.8	0.8	0	0.7	0.7	0.9	0.8	1.0	1.3	0.8	0.8
Sediment input: decrease	0.1	0	0.8	0.6	1.6	1.2	2.3	0.8	2.4	0.3	0	0.4	0
Sediment input: increase	1.4	1.1	1.3	0.8	1.4	1.8	1.4	1.5	1.4	0	0	1.2	0
Shipping (commercial, cruise, etc.)	0	0.3	0.3	0	0	1.4	0.4	0.2	0	0.3	0	0	0
Tourism: kayaking	0.6	0.5	0.1	0	0	0.4	0.4	0.4	0.2	0.1	0	0	0
Tourism: recreational boating	0.9	1.0	1.0	0	0	0.2	0.8	0	0.2	0.2	0	0	0.4
Tourism: scuba diving	1.0	0.9	0.1	0	0	0	0	0	0	0.1	0	0	0.2
Tourism: surfing	0	0	0.1	0	0	0.4	0	0.6	0	0	0	0	0
Score mean	0.8	0.9	0.8	0.4	1.0	1.1	1.1	1.0	1.0	0.7	0.5	0.5	0.7
Score SE	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1
Sample size mean	11.5	9.3	9.5	3.8	0.2	3.8	5.2	13.1	8.0	6.1	1.7	2.1	3.1
Sample size SE	0.1	0.1	0.1	0.1	0.0	0.1	0.1	0.2	0.1	0.1	0.0	0.0	0.1

Notes: Mean scores for each stressor across all ecosystems, and for each ecosystem across all stressors, are reported in the "score mean" column and row, respectively. Ecosystem abbreviations: KF (kelp forest), RR (rocky reef), SG (seagrass), Shl (shallow soft), SR (suspension-feeding reefs), BE (beach), MF (mud flats), RI (rocky intertidal), SM (salt marsh), SSh (soft shelf), SSl (soft slope), SD (soft deep), HSh (hard shelf), HSl (hard slope), HD (hard deep), Cyn (canyons), SMt (seamounts), Surf (surface waters), Deep (deep waters). Score identities are based on four equal divisions of the range of values: 0.0–0.8 (normal black font), 0.9–1.7 (light blue), 1.8–2.6 (purple), and 2.7–3.4 (red). Sample size means (±SE) were calculated based on the average sample size per vulnerability criteria in Part IV (i.e., when a respondent evaluated a stressor, all vulnerability criteria values were not always provided). Stressor abbreviations: acidific. (acidification), alt. (altered), byc. (bycatch), demrs. (demersal), des. (destructive), dynam. (dynamics), engineer. (engineering), expts. (experiments), HABs (harmful algal blooms), hyp. (hypoxic), meso. (mesotrophic), temp. (temperature).

Table 6. Extended.

Offshore ecosystems						
HSl	HD	Cyn	SMt	Surf	Deep	Score mean
0	0	0	0	0	0	0
0	0	0	0	1.2	0	0.3
0	0	0	0	0	0	0.1
0	0	0	0	0.2	0	0.4
2.3	0	2.3	0	0.4	0	1.4
2.3	3.4	2.6	2.6	3.2	2.7	2.6
0	0	0	0	0	0.6	0.9
1.2	0	1.7	0	2.5	1.9	1.5
0	0	0	0	2.5	0.8	0.9
0	0	0	0	0	0	0.7
0	0	0	0	0.2	0	0.8
0	0	0	0	0	0	0.3
1.2	0	1.1	0	0.5	0	0.7
0	0	0	0	0.1	0	0.5
0	0	0	0	0	0	0.1
2.3	2.8	2.5	2.7	0.3	0	1.3
1.8	1.3	1.3	1.3	0.4	0	1.0
1.1	0.9	0.8	0.9	0.3	0	0.8
0	0	0	0	0.1	0	0.2
0	0	0	0	0.1	0	0.3
0	0	0	0	1.6	1.6	0.3
0	0	0	0	1.1	1.5	0.2
1.6	0.7	0	0.7	1.1	0	0.9
0	0	0	0	0.1	0	0.3
0	0	0	0	1.0	0	0.5
0	0	0	0	0.3	0	1.2
0	0	0	0	0	0	0.2
1.3	1.3	1.3	1.2	1.4	1.4	1.0
1.3	0	0	0	1.5	1.8	1.0
1.0	0	0	0	1.8	2.0	1.0
0	0	1.0	0	1.1	0.9	0.8
0	0	1.3	0	1.4	2.1	0.9
1.2	1.3	1.2	1.3	1.3	1.3	1.1
1.0	0.9	0.6	0.7	1.0	0.8	0.8
2.5	2.5	2.3	2.3	0	0	1.6
1.4	1.1	1.3	1.1	1.1	1.3	1.2
0	0	0	0	0	0	0.2
1.3	0	0.9	0	1.4	0	0.7
0.7	0	1.3	0	1.6	0.9	0.8
0	0	1.3	0	1.6	1.3	1.2
0	0	0	0	0.4	0.8	0.4
0	0	1.2	0	1.5	1.3	1.3
0.9	0	0.8	0	1.1	0.8	0.9
0	0	0	0	1.5	0.2	0.6
0	0.7	0.7	0.7	0.7	0.4	0.6
0	0.9	0.9	0.9	1.0	0.5	0.8
0	0	0	0	0	0	0.6
1.0	0	1.4	0	0.2	0	0.8
0	0	0	0	1.5	0	0.2
0	0	0	0	0.9	0	0.2
0	0	0	0	1.1	0	0.3
0	0	0	0	0.2	0	0.1
0	0	0	0	0.2	0	0.1
0.5	0.3	0.6	0.3	0.8	0.5	0.7
0.1	0.1	0.1	0.1	0.1	0.1	0.07
2.2	1.0	0.7	1.9	11.6	1.8	19.0
0.1	0.0	0.0	0.0	0.1	0.0	0.00

Table 7. Scores and rank orders for directly stated top stressors (Part II) and the multi-criteria decision model (MCDM) (based on Parts III and IV).

Stressor	Directly stated		MCDM for all ecosystems		Coastal MCDM		Offshore MCDM	
	Score	Rank order	Score	Rank order	Score	Rank order	Score	Rank order
Aquaculture: finfish (herbivores)	0.01	40	0.00	53	0.00	53	0.00	52
Aquaculture: finfish (predators)	0.01	42	0.27	40	0.19	50	0.33	28
Aquaculture: marine plant	0.00	51	0.10	51	0.21	48	0.0	53
Aquaculture: shellfish	0.10	19	0.41	36	0.83	30	0.04	42
Benthic structures: e.g., oil rigs	0.03	33	1.37	4	1.64	6	1.14	8
Climate change: ocean acidification	0.11	18	2.57	1	2.19	2	2.91	1
Climate change: sea level rise	0.06	25	0.88	18	1.80	4	0.06	40
Climate change: sea temperature change	0.42	1	1.54	3	1.91	3	1.20	6
Climate change: UV change	0.01	43	0.93	15	1.59	7	0.33	29
Coastal engineering: altered flow dynamics	0.19	11	0.71	27	1.48	9	0.02	46
Coastal engineering: habitat alteration	0.32	3	0.81	23	1.66	5	0.04	43
Direct human impact: trampling	0.15	13	0.33	37	0.67	34	0.01	49
Disease/pathogens	0.12	17	0.70	28	0.94	25	0.48	24
Dredging	0.08	22	0.54	33	1.06	20	0.07	38
Fishing: aquarium	0.01	41	0.13	50	0.26	45	0.02	47
Fishing: demersal destructive	0.20	6	1.30	5	0.66	35	1.87	2
Fishing: demersal nondestructive high bycatch	0.19	10	1.01	11	0.90	26	1.13	9
Fishing: demersal nondestructive low bycatch	0.20	7	0.80	24	0.84	29	0.76	16
Fishing: destructive artisanal	0.04	29	0.24	46	0.48	41	0.01	50
Fishing: nondestructive artisanal	0.05	26	0.27	41	0.52	39	0.03	44
Fishing: pelagic high bycatch	0.12	15	0.29	39	0.22	46	0.35	27
Fishing: pelagic low bycatch	0.07	23	0.25	43	0.16	51	0.32	30
Fishing: recreational	0.33	2	0.85	19	1.09	17	0.65	21
Freshwater input: decrease	0.01	46	0.26	42	0.54	38	0.01	51
Freshwater input: increase	0.02	36	0.51	34	0.89	27	0.18	33
Invasive species: from ballast, etc.	0.22	5	1.25	7	2.23	1	0.36	26
Marine component of forestry operations (log booms)	0.03	34	0.25	45	0.48	40	0.03	45
Military activity	0.01	50	0.96	14	0.59	36	1.29	4
Nutrient input: causing harmful algal blooms	0.14	14	1.00	12	1.33	12	0.71	17
Nutrient input: causing hypoxic zones	0.07	24	1.00	13	1.22	14	0.81	14
Nutrient input: into eutrophic (upwelled) waters	0.09	21	0.78	25	1.07	19	0.52	23
Nutrient input: into mesotrophic (non-upwelled) waters	0.05	27	0.91	17	1.14	16	0.69	18
Ocean dumping: lost fishing gear	0.04	32	1.13	10	1.01	23	1.25	5
Ocean dumping: marine debris, trash, etc.	0.04	31	0.82	22	0.80	31	0.85	12
Ocean dumping: ship wrecks	0.00	52	1.61	2	1.56	8	1.67	3
Ocean dumping: toxic materials	0.02	37	1.15	8	1.16	15	1.17	7
Ocean mining: sand, minerals, etc.	0.00	53	0.25	44	0.20	49	0.29	31
Ocean pollution: chemicals from ships, ports, spills	0.16	12	0.69	29	0.86	28	0.54	22
Pollution input: atmospheric	0.01	44	0.84	20	1.01	22	0.68	20
Pollution input: inorganic	0.12	16	1.15	9	1.23	13	1.08	11
Pollution input: light/noise	0.02	39	0.43	35	0.76	32	0.14	36
Pollution input: organic	0.20	9	1.29	6	1.48	10	1.13	10
Pollution input: trash, etc. (i.e., urban runoff)	0.20	8	0.91	16	1.04	21	0.80	15
Power, desalination plants	0.05	28	0.55	32	0.96	24	0.19	32
Scientific research: collecting	0.01	47	0.63	30	0.58	37	0.68	19
Scientific research: experiments/surveys	0.02	38	0.75	26	0.69	33	0.81	13
Sediment input: decrease	0.09	20	0.56	31	1.09	18	0.07	39
Sediment input: increase	0.22	4	0.83	21	1.34	11	0.38	25
Shipping: commercial, cruise, ferry	0.01	45	0.22	47	0.29	43	0.18	34
Tourism: kayaking	0.01	48	0.20	48	0.29	44	0.10	37
Tourism: recreational boating	0.04	30	0.30	38	0.46	42	0.17	35
Tourism: scuba diving	0.03	35	0.13	49	0.22	47	0.05	41
Tourism: surfing	0.01	49	0.07	52	0.12	52	0.02	48

Notes: Directly stated scores were calculated based on the frequency of each stressor occurring among the top five stated stressors across all ecosystems; average ranks were used to break ties. The multi-criteria decision model score was calculated from Eq. 1 for each ecosystem and then averaged across all ecosystems, and for coastal and offshore ecosystems separately.

Appendix A

Sample survey for a kelp forest ecosystem is provided, except that Part III for both coastal and offshore ecosystems is included to show where scenario names were changed between these two expert groups.

NCEAS

NATIONAL CENTER FOR
ECOLOGICAL ANALYSIS AND SYNTHESIS

RANKING AND MAPPING THE IMPACT OF HUMAN ACTIVITIES IN CALIFORNIA CURRENT MARINE ECOSYSTEMS

This research project, "Ranking and mapping human threats and impacts to marine ecosystems in the California Current," is designed to evaluate, rank and map the range and effect of human activities on marine ecosystems within the California Current, from the U.S.-Canada border to Baja, Mexico. The project is funded by the Betty and Gordon Moore Foundation, and being conducted by researchers at the National Center for Ecological Analysis and Synthesis, Stanford University, and the Nature Conservancy. The project will combine the input of marine scientists familiar with the California Current to create a visual map detailing how particular activities affect different ecosystems within the area.

For this survey we will ask about your background, experience and training, and then ask you to evaluate the impact of various human activities with regard to the ecosystem(s) you research. There are no right or wrong answers; we are asking for your informed assessment. The survey should take about 30-45 minutes to complete.

The survey is confidential, and responses of those surveyed will be assigned a number and securely stored. The list of participants will be shared only within a small number of other researchers involved in the project.

Your participation is of course voluntary. Please understand that by returning the survey to us you are agreeing to take part in this study.

We thank you in advance for your time and assistance.

The proposal for this research has been approved by the Human Subjects Office at UC Santa Barbara. If you have any questions, you may contact Kathleen Graham at graham@research.ucsb.edu

PROJECT OVERVIEW:

This project aims to understand and map how human activities are affecting marine ecosystems in the California Current, a region defined in this study as the coastal marine area between the U.S.-Canada border and central Baja, Mexico. The project builds upon previous work by collaborators from the National Center for Ecological Analysis and Synthesis (NCEAS) and Stanford University, which mapped human impacts on marine ecosystems globally. As part of the current project we are conducting a survey of marine experts to better gauge the distinct ways in which activities affect different marine ecosystems. Guidelines for contributing to the survey are intended to make the process quantifiable, repeatable, and transparent.

For this project, we are focused on **present-day (within the past five years)** human influences on particular ecosystems within the California Current. We therefore ask you to think about influences as they are manifested today, rather than their projected impact in the future. The survey includes four parts: first, we will ask about your background, experience and training; second, based upon your region(s) of expertise, we will ask you to list which human activities are having the biggest impact on specific ecosystem(s) you research; third, we will ask you to rank the severity of certain human activities based upon ecosystem vulnerability scores that we will provide; and, fourth, we will ask you to consider and revise the vulnerability scores we have for your specific ecosystem(s), determined through a previous study. Concepts and terms will be explained throughout the survey, but feel free to ask any clarifying questions. The survey should take about 45 minutes to complete.

PART I: BACKGROUND, EXPERIENCE AND TRAINING

Name: _____

Email address: _____

Main affiliation: _____

Other affiliations: _____

Type of position *(please check one of the following)*:

☐ academic ☐ agency (federal) ☐ non-governmental organization

Age: _____

Gender: _____

Ethnicity *(please check all that apply)*:

☐ African American/Black
☐ American Indian/Alaskan Native
☐ Asian, or Pacific Islander
☐ Caucasian/White
☐ Hispanic/Latino
☐ Other

Highest degree earned: _____

Year of degree: _____

Years of scientific experience within each geographic region *(please note the number of years in each space provided, **including zero for no experience**)*:

☐ Washington

☐ Oregon

☐ Northern California (San Francisco and North)

☐ Central California (South of San Francisco and North of Point Conception)

☐ Southern California (South of Point Conception)

☐ Baja California (North of Punta Eugenia)

Which geographic region(s) do you want to focus on for this survey? Please check one or more of the boxes below. *If checking multiple regions please let us know whether you think human activities affect these areas differently, so that we may provide any needed additional forms.*

☐ Washington

☐ Oregon

☐ Northern California (San Francisco and North)

☐ Central California (South of San Francisco and North of Point Conception)

☐ Southern California (South of Point Conception)

☐ Baja California (North of Punta Eugenia)

If you do not feel qualified to discuss an entire region, please list the specific location(s) you want to consider:

Years of scientific experience within each ecosystem listed below *(please note the number of years in each space provided, **including zero for no experience**)*:

SUBTIDAL COASTAL:
- ☐ kelp forest
- ☐ rocky reef
- ☐ seagrass
- ☐ shallow soft
- ☐ suspension reefs

INTERTIDAL:
- ☐ beach
- ☐ mud flats
- ☐ rocky intertidal
- ☐ salt marsh

OFFSHORE:
- ☐ soft shelf
- ☐ soft slope
- ☐ soft deep
- ☐ hard shelf
- ☐ hard slope
- ☐ hard deep
- ☐ canyons
- ☐ seamounts
- ☐ vents/seeps
- ☐ surface waters (top 100 m)
- ☐ deep (aphotic, pelagic)

Based upon the greatest years of experience marked above, please list which ecosystem(s) you would like to focus on for this survey. (If you have expertise in multiple ecosystems, please let us know so that we may provide you the needed additional forms):

Kelp Forest

PART II: RANKING IMPACT OF ACTIVITIES (5 MINUTES) KELP FOREST

1	Nutrient input: causing harmful algal blooms
2	Nutrient input: causing hypoxic zones
3	Nutrient input: into oligotrophic waters
4	Nutrient input: into eutrophic waters
5	Ocean mining (sand, minerals, etc.)
6	Shipping (commercial, cruise, ferry)
7	Pollution input: organic
8	Pollution input: inorganic
9	Pollution input: atmospheric
10	Pollution input: trash, etc. (urban runoff)
11	Pollution input: light/noise
12	Direct human impact: trampling
13	Coastal engineering: habitat alteration
14	Coastal engineering: altered flow dynamics
15	Military activity (i.e. sonar testing)
16	Power, desalination plants
17	Fishing: demersal destructive
18	Fishing: demersal non-destructive low bycatch
19	Fishing: demersal non-destructive high bycatch
20	Fishing: pelagic low bycatch
21	Fishing: pelagic high bycatch
22	Fishing: aquarium
23	Fishing: recreational
24	Fishing: destructive artisanal
25	Fishing: non-destructive artisanal
26	Marine component of forestry operations (log booms,
27	Ocean dumping: marine debris (trash, etc.)
28	Ocean dumping: toxic materials
29	Ocean dumping: lost fishing gear
30	Ocean dumping: ship wrecks
31	Sediment input: increase
32	Sediment input: decrease
33	Dredging
34	Invasive species (from ballast, etc.)
35	Scientific research: collecting
36	Scientific research: experiments/surveys
37	Benthic structures (e.g. oil rigs)
38	Tourism: scuba diving
39	Tourism: recreational boating
40	Tourism: kayaking
41	Tourism: surfing
42	Aquaculture: marine plant
43	Aquaculture: shellfish
44	Aquaculture: finfish (herbivores)
45	Aquaculture: finfish (predators)
46	Ocean pollution (oil, chemicals, etc from ships, ports,
47	Freshwater input: increase
48	Freshwater input: decrease
49	Disease/pathogens
50	Climate change: sea temperature change
51	Climate change: UV change
52	Climate change: ocean acidification
53	Climate change: sea level rise

Based upon the activities listed here, please rank from 1-5 those you consider to be affecting your chosen region and ecosystem most, with 1 having the largest impact. Please do not take more than five to ten minutes for this section.

1. _____

2. _____

3. _____

4. _____

5. _____

Please list any activities affecting your ecosystem that are not listed, and whether they would be among your top five impacts:

_____

_____

_____

_____

_____

_____

_____

_____

_____

_____

PART III: RANKING IMPACT OF ACTIVITIES BASED ON VULNERABILITY (15-20 MINUTES)

VULNERABILITY DEFINITION:

The Millennium Ecosystem Assessment's Condition and Trends Working Group defines vulnerability as incorporating three major components:

> [1] exposure to stresses, perturbations, and shocks; [2] the sensitivity of people, places, and ecosystems to stress or perturbation, including their capacity to anticipate and cope with the stress; [3] and the resilience of exposed people, places, and ecosystems in terms of their capacity to absorb shocks and perturbations while maintaining function.

Drawing upon this definition, we consider ecosystem vulnerability to encompass both the impact of human activities on marine ecosystems, measured by their ***spatial extent***, ***frequency*** and ***trophic impact***, and their impact on the ecosystem, measured as ***percent change*** of trophic levels affected (i.e. ecosystem resistance), and its resilience or ***recovery time*** from the impact. These five factors and the ranking system we use for each are defined and discussed in more detail below.

Each ecosystem-by-activity combination likely has a unique vulnerability score due to the differential way in which ecosystems respond to perturbations. These are the scores that we are trying to develop with this survey. We are focused on the total impacts of human activities on marine ecosystems, including both direct (e.g. species mortality) and indirect (e.g. nursery habitats like mangroves) effects leading to the loss or impairment of species or whole ecosystems. The distinction between these effects will not be captured in the survey, but may be the subject of later analyses. We recognize that most places are affected by multiple human activities and that the effect of these activities is often multiplicative rather than simply additive. Taking the most conservative course, we plan to account for only the individual effects of activities.

VULNERABILITY MEASURES

Spatial extent – *the spatial scale at which a single act of an activity impacts the ecosystem, both directly and indirectly, measured in* km^2. The measurement reflects the scale of a *single* event of the activity, not the cumulative or aggregate effect of the activity type. For example, a single pass of a demersal trawl may cover roughly 1-10 km^2, while all demersal trawling impacts thousands of km^2 of continental shelf ecosystem each year. The first scale is what we are interested in, as the second scale will be captured by our efforts to map the distribution of trawling across the region. Consider another example where dredging or construction of a bridge across a bay mouth directly impacts only a small area but dramatically affects tidal flow into the bay. In this case, the scale of the activity would be the entire bay.

Frequency – *the average annual frequency (days per year) of the activity at a particular location within a given region*. Consider a case where fishing of top predators occurs everywhere within a region, but only affects a particular location twice a year. The frequency in this case would be twice per year. It is important to note that frequency is not a measure of duration, so even though this fishing only happens on average twice per year, the consequences of it may persist for years. The consequences, or duration, will be captured in the recovery time category below. In the few cases where an activity has permanently altered an ecosystem or part of an ecosystem, the frequency of that activity should be counted as every day of the year (e.g. 365), given its daily impact. Fractions represent times longer than a single year (e.g. 1/10 = once a decade).

Trophic impact – *the primary level of marine life affected by an activity within a given ecosystem and region*. Trophic impact is scored on the following scale:

0: N/A (No impact or positive)
1: Species (single or multiple)
2: Single trophic level
3: > 1 trophic level
4: Entire community, including associated habitat structure

For example, while change-induced acidification may primarily affect corals and other carbonate skeleton-building organisms, its trophic impact would rank as a 4 given that these organisms provide biogenic habitat upon which many other species depend. Similarly, fishing that affects a key species or group of species may be considered an impact to the entire community if it is known to lead to broad-scale trophic cascades. "Species" can be used for single or multiple species—e.g. ship strikes impact several species of whales. Single and multiple trophic level ranks connote that the activity broadly impacts multiple species within or across trophic level(s) but does not disrupt the entire ecosystem. For example, recreational boating may impact many species of sessile invertebrates within the same trophic level without cascading effects to the rest of the ecosystem (single trophic level), while hook-and-line fishing may remove huge numbers of species from several trophic levels but leave the habitat structure and associated plant and algal biomass intact (>1 trophic level).

Percent change – *the degree to which the species, trophic level(s), or entire ecosystem's 'natural' state is impacted by the activity*. What is the average tendency of the selected trophic component to change due to a given activity, or put another way how poor is its resistance to that activity? 0% indicates no effect on abundance, and 100% indicates the trophic component is completely removed.

Recovery time – *the average time (in years) required for the affected species, trophic level(s), or entire community to return to its former, 'natural' state following disturbance by a particular activity*. Fractions represent times shorter than a single year.

RANKING ACTIVITIES USING OUR PROVIDED VULNERABILITY MEASURES:

On the following page, please rank the activities by their severity of impact based upon the vulnerability measures provided. We ask you to determine and rank the five activities with the biggest impact (1-5), and also the five activities with the smallest impact (26-30), with 1 indicating the biggest impact and 30 the smallest. You may stop ranking at this point, or continue ranking top and bottom activities (i.e. 6-25). The rankings will be used to create a predictive model for assessing the overall ecological impact of human activities when vulnerability measures are known. We will give you the opportunity to revise the vulnerability measures for your region(s) and ecosystem(s) of expertise in Part IV of the survey.

RANKING THESE THREATS SHOULD TAKE ABOUT 10-15 MINTUES

Please rank the activities listed below by their severity of impact based upon the vulnerability measures provided—the five activities with the biggest impact (1-5) and the five activities with the smallest impact (26-30). **Please do not think of your chosen region and ecosystem,** as the numbers represent a ***hypothetical coastal [or offshore] ecosystem*** in a ***hypothetical region***. It is important that your rankings are based solely upon the vulnerability measures provided.

Coastal	Offshore	Spatial extent (km^2)	Frequency (#/yr)	Trophic impact (level)	Percent change (%)	Recovery time (yrs)
Aquaculture: marine plant	Aquaculture: finfish (predators)	2	360	1	20%	1
Aquaculture: shellfish	Shipping (commercial, cruise, ferry)	5	360	1	5%	0.1
Climate change: sea level rise		10000	1/2	2	20%	5
Climate change: sea temperature change		50000	1	3	25%	50
Climate change: UV change		10000	1/10	1	5%	1
Coastal engineering: habitat alteration	Ocean mining (sand, minerals, etc.)	1	1	4	75%	25
Direct human impact: trampling	Disease/pathogens	150	360	2	35%	25
Fishing: demersal destructive		8	1/20	4	10%	0.5
Fishing: demersal non-destructive low bycatch		0.1	1/20	1	10%	0.5
Fishing: non-destructive artisanal	Fishing: demersal non-destructive high bycatch	1	1/20	1	50%	1
Fishing: pelagic high bycatch		5	1/100	1	5%	0.5
Fishing: recreational		8	52	2	20%	5
Freshwater input: increase	Fishing: pelagic low bycatch	10	1/5	2	10%	1
Invasive species (from ballast, etc.)		20000	360	1	25%	20
Military activity (i.e. sonar testing)		10	12	1	10%	5
Nutrient input: causing harmful algal blooms		100	1/5	2	10%	1

PART IV. REVISING VULNERABILITY MEASURES: (15-30 MINUTES)

The following pages list estimated vulnerability scores, determined from a previous study conducted at a global scale, for the ecosystem of your expertise. We would appreciate your expertise in adapting these scores to the California Current. Please use the same approach to evaluating vulnerability as you used in Part III; the vulnerability scores capture the nature of an activity where it exists. Drawing upon your experience in the region(s) where you work, we ask you to:

1. Review the vulnerability measures.
2. Mark a √ in the column labeled "agree" for those activities that you agree with all 5 vulnerability scores.
3. Revise any vulnerability measures you disagree with in the blank space next to each value.
4. If you are unable to assess a particular indicator (due to data gaps or uncertainty) please write "don't know" in the space next to the provided value.
5. Mark a √ in the column labeled "don't know" if you review a row and feel that you are not qualified to review the vulnerability measures or if you believe more scientific information is required to verify the vulnerability measures.
6. If an activity does not affect your ecosystem, please consider all scores to be "0."

In all cases, please use your best judgment, drawing on published and unpublished empirical data, experiments, reviews, and personal experience in the field to assess vulnerability of your study ecosystem.

If you do not feel qualified to discuss an entire region, please feel free to list specific locations you want to consider:

FOR KELP FOREST ECOSYSTEM:

Activity Name	Spatial extent (km^2)	Frequency (#/yr)	Trophic Impact (level)	Percent change (%)	Recovery Time (yrs)	agree? √	don't know? √
Freshwater input: increase	10	2	1	10%	0.5		
Freshwater input: decrease	0	0	0	0%	0		
Sediment input: increase	25	4	2	10%	1		
Sediment input: decrease	0	0	0	0%	0		
Nutrient input: into mesotrophic (non-upwelled) waters	25	4	1	20%	2		
Nutrient input: into eutrophic (upwelled) waters	10	1	1	5%	1		
Nutrient input: causing harmful algal blooms	100	1/10	1	20%	2		
Nutrient input: causing hypoxic zones	200	1/10	3	30%	5		
Pollution input: organic	50	12	1	10%	2		
Pollution input: inorganic	50	6	1	20%	5		
Pollution input: atmospheric	100	12	1	10%	2		
Pollution input: trash, etc. (urban runoff)	0.1	24	1	1%	0.1		
Pollution input: light/noise	0	0	0	0%	0		
Coastal engineering: habitat alteration	0	0	0	0%	0		
Coastal engineering: altered flow dynamics	0	0	0	0%	0		
Direct human impact: trampling	0	0	0	0%	0		
Disease/pathogens	20	1/10	1	20%	5		

Activity Name	Spatial extent (km^2)	Frequency (#/yr)	Trophic Impact (level)	Percent change (%)	Recovery Time (yrs)	agree? √	don't know? √
Aquaculture: marine plant	0	0	0	0%	0		
Aquaculture: shellfish	0	0	0	0%	0		
Aquaculture: finfish (herbivores)	0	0	0	0%	0		
Aquaculture: finfish (predators)	0	0	0	0%	0		
Fishing: demersal destructive	0	0	0	0%	0		
Fishing: demersal non-destructive low bycatch	0.1	3	1	10%	2		
Fishing: demersal non-destructive high bycatch	0.1	6	2	20%	5		
Fishing: pelagic low bycatch	0	0	0	0%	0		
Fishing: pelagic high bycatch	0	0	0	0%	0		
Fishing: aquarium	1	1/10	1	10%	2		
Fishing: recreational	2	12	1	25%	5		
Fishing: destructive artisanal	0	0	0	0%	0		
Fishing: non-destructive artisanal	0	0	0	0%	0		
Marine component of forestry operations (log booms, etc.)	0	0	0	0%	0		
Scientific research: collecting	0.1	4	1	10%	2		
Scientific research: experiments/surveys	1	3	1	1%	0.1		
Ocean mining (sand, minerals, etc.)	0	0	0	0%	0		
Dredging	0	0	0	0%	0		

Activity Name	Spatial extent	Frequency	Trophic Impact	Percent change	Recovery Time	agree?	don't know?
	(km^2)	(#/yr)	(level)	(%)	(yrs)	√	√
Shipping (commercial, cruise, ferry)	0	0	0	0%	0		
Benthic structures (e.g. oil rigs)	1	360	4	100%	10		
Ocean dumping: marine debris (trash, etc.)	0.1	2	1	5%	0.1		
Ocean dumping: toxic materials	10	1/5	1	20%	10		
Ocean dumping: lost fishing gear	2	1/2	2	20%	5		
Ocean dumping: ship wrecks	1	360	3	50%	10		
Tourism: scuba diving	2	12	1	5%	0		
Tourism: recreational boating	5	12	1	5%	0.5		
Tourism: kayaking	3	6	1	1%	0.01		
Tourism: surfing	0	0	0	0%	0		
Power, desalination plants	0	0	0	0%	0		
Military activity	500	2	1	10%	20		
Ocean pollution (oil, chemicals, etc from ships, ports, spills, etc.)	10	2	1	10%	3		
Invasive species (from ballast, etc.)	100	360	1	10%	20		
Climate change: sea temperature change	10000	360	2	20%	5		
Climate change: UV change	10000	360	1	10%	10		
Climate change: ocean acidification	10000	360	3	30%	25		
Climate change: sea level rise	10000	360	1	5%	1		

Part V. *SUPPLEMENTARY INFORMATION: (5 MINUTES)*

1. Please identify any differences in the reasoning for your ranking decisions in Part II (chose top 5 activities from the full list) versus Part III (rank top 5 and bottom 5 activities using vulnerability criteria scores). For example, did your criteria for ranking the threats differ?

2. If you were to refine the criteria we used to assess and measure ecological vulnerability, how would you do that? This could include criteria that you would add, omit or revise.

3. Comments or questions?

Appendix B

Number of surveys completed per ecosystem per region and subtotals per ecosystem and region.

	WA	OR	N CA	Cen CA	S CA	Baja CA	TOTAL
kelp	1	1	2	9	13	1	**27**
rocky reef	1	6	3	6	4	1	**21**
seagrass	6	2	6	2	6	4	**26**
shallow soft	0	0	1	3	3	3	**10**
suspension reefs	1	1	1	1	1	0	**5**
beach	1	1	1	1	5	1	**10**
mud flats	3	3	4	5	4	1	**20**
rocky intertidal	6	4	3	7	7	3	**30**
salt marsh	3	4	2	3	5	1	**18**
soft shelf	5	5	3	6	2	1	**22**
soft slope	1	1	2	3	0	0	**7**
soft deep	0	0	1	3	1	0	**5**
hard shelf	1	2	2	3	2	0	**10**
hard slope	3	3	2	1	1	0	**10**
hard deep	1	0	1	1	1	0	**4**
canyons	0	0	0	2	0	0	**2**
seamounts	1	2	1	1	1	0	**6**
vents/seeps	0	0	0	0	0	0	**0**
surface waters	7	7	4	9	10	4	**41**
deep waters	1	1	1	2	2	0	**7**
TOTAL	**42**	**43**	**40**	**68**	**68**	**20**	**281**

Appendix C

Respondents' average years of experience ±SE per chosen ecosystem (Table C1)and per chosen subregion (Table C2). The sample size, N, represents the number of respondents reporting years of experience within that chosen subregion or ecosystem (note: some respondentsapplied surveys to more than one ecosystem or subregion).

Table C1.

	average	N	±SE
kelp	17.5	19	2.7
rocky reef	11.1	14	2.6
seagrass	13.6	15	2.7
shallow soft	13.8	7	5.1
suspension reefs	8.0	1	--
beach	15.2	9	3.6
mud flats	12.6	11	2.8
rocky intertidal	17.9	22	2.2
salt marsh	8.0	14	1.8
soft shelf	13.7	11	3.1
soft slope	20.3	3	7.6
soft deep	24.5	4	4.9
hard shelf	12.8	5	6.7
hard slope	17.5	2	12.5
hard deep	5.0	1	--
canyons	16.8	2	10.8
seamounts	6.5	2	3.5
vents/seeps	--	--	--
surface waters	14.5	15	2.9
deep waters	26.0	2	6.0

Table C2.

	average	N	±SE
Washington	15.7	41	1.7
Oregon	10.5	42	1.0
northern California	12.1	37	1.2
central California	15.3	56	1.4
southern California	15.8	59	1.4
Baja California	10.4	17	1.3

Appendix D

Threats listed by participants in the survey that were not on our stressor list.

aircraft: general disturbance
benthic structures: underwater cables
boating: anchor damage
boating: general disturbance
climate change: altered oceanographic regimes (e.g., wind, circulation, or upwelling)
climate change: global temperature change (not just sea temperature change)
coastal and inland engineering: alteration of tributaries and watersheds
coastal engineering: agricultural diking and ditching
coastal engineering: beach grooming
coastal engineering: clearing vegetation for agriculture or development
coastal engineering: housing particularly on dunes and cliffs
energy development: oil exploration and drilling (as distinguished from oil rigs and ocean mining)
energy development: wave and tide driven power plants
fires, charcoal, fireworks
fishing: causing trophic cascades
fishing: commercial (as a broad category)
hypoxia not exclusively caused by nutrient input
illegal harvesting (poaching or harvesting by public)
kelp harvesting
mining for sand
non-toxic algal blooms
nutrient input: due to upwelling
overpopulation
pollution: heavy metals
pollution: pesticides
scientific research: non-destructive surveys (e.g., ROVs or AUVs)
sea temperature change from El Nino events
sea temperature change from power plant effluent
tourism: all-terrain and off-road vehicles
tourism: beach recreation
tourism: unleashed dogs
tourism: whale watching
trophic interactions (e.g., predation from recovered marine mammals)

II. Disentangling the effects of fishing and environmental forcing on demographic variation in an exploited species

Collaborators: Julio Lorda, Thomas Bell, Jorge Cornejo-Donoso, Jenn E. Caselle, Scott L. Hamilton, Nick T. Shears, Steven D. Gaines

Abstract

Species targeted by fishing activities often recover in abundance and size structure when afforded protection within marine protected areas (MPAs). The associated increase in reproductive potential within MPA boundaries has been suggested as one mechanism by which MPAs can enhance population replenishment and thereby benefit fisheries. However, in some situations, concomitant changes in the abundance of predators, competitors, or prey within MPAs or strong gradients in the surrounding environmental seascape may counteract the purported benefits, which can make it more difficult to predict how the demography of key species will respond to protection. Marine protected areas arrayed over a biogeographic cline provide an opportunity to test how demographic variability may be shaped by the potentially interactive effects of protection from fishing and spatial differences in environmental forcing. We used a network of MPAs established in 2003 in California's Northern Channel Islands to investigate the drivers of demographic

variability on one of the most important exploited species in California, the red sea urchin *Mesocentrotus franciscanus*. The MPA network exists across a striking east-west biogeographic gradient. Given this setting, we investigated how reproductive condition and other urchin demographic metrics varied geographically in response to protection (MPA vs unprotected areas), temperature, and the main urchin resource, the giant kelp *Macrocystis pyrifera*. Biomass and mean size of red sea urchin adults were greater within MPAs, and consequently reproductive biomass was elevated in reserve locations. Kelp density was an important explanatory variable of all red sea urchin demographic traits (size, gonadosomatic index [GSI], density, biomass, and reproductive biomass). Kelp density was positively correlated with GSI and urchin size, but the relationships with density, biomass, and reproductive biomass were complex and the directionality changed depending on the region (or environmental setting) examined. In addition, red sea urchin adult size and reproductive biomass were higher in the western, cooler region. We observed a number of complex interactions, notably that urchin adult biomass and reproductive biomass were positively related with kelp but only in warmer areas within the region. Our results demonstrate that kelp, red sea urchin reproduction, and consequently protection from fishing are tightly coupled with the varying oceanographic regime across the Channel Islands. We not only provide key baseline demographic data for an important fished species within a heavily fished region but also underscore both the major impacts from humans as predators and the significant benefits from species protection.

Keywords: kelp forest; marine protected area; marine reserves; Channel Islands; sea urchins; sea urchin fishery; *Mesocentrotus franciscanus*; *Macrocystis pyrifera*

Introduction

Understanding the ecological, environmental, and anthropogenic factors that control spatial variation in population demography allows for more accurate forecasting that can benefit resource management. Marine species are fished from wild populations that typically span broad spatial expanses over which biological traits of the species often vary. Biological variation in life history and demographic traits can occur in response to geographic or temporal shifts in temperature, productivity, resource availability, competition, and predation (including fishing pressure) (Paine 1980; Menge & Sutherland 1987; Polis & Hurd 1996; Castilla 1999; Menge 2000; Ruttenberg *et al.* 2005; Rogers-Bennett 2007; Darimont *et al.* 2009; Bolnick *et al.* 2010; Lorda & Lafferty 2012; Bonel *et al.* 2013; Lorda 2014; Bonel & Lorda 2015). While stock assessments have usually assumed that biological parameters such as growth, maturation or reproductive output are consistent across space, recent studies have shown that incorporating spatial variation in life histories into fisheries models and assessments can be useful for resource management (Wilson *et al.* 2010; Wilson *et al.* 2012; Caselle *et al.* 2011; Hamilton *et al.* 2011; Teck *et al.* in preparation). Understanding the drivers that may lead to spatial variation in key population parameters allows for better predictions concerning how

species will respond in the future to changes that may result from climate change or new management regulations (Harley *et al.* 2006).

Previous research has shown that reproduction of targeted species often is greater within reserves. Similar to effects from natural predation (Chesness *et al.* 1968; Magnhagen 1991; Schwarzkopf & Shine 1992; Durant 2000), harvesting by humans can reduce the reproductive success of targeted species. Harvesting wild species may result in lower reproductive rates than in adjacent non-harvested regions within many different global ecosystems, from terrestrial habitats (Witkowski *et al.* 1994; Novaro *et al.* 2000; Hackney & McGraw 2001) to subtidal marine habitats (Beukers-Stewart *et al.* 2005). Reproductive potential is often higher within marine protected areas (MPAs) due to the presence of larger and older individuals (Allison, Lubchenco & Carr 1998; Rogers-Bennett *et al.* 2002; Gell & Roberts 2003; Tetreault & Ambrose 2007; Wilson *et al.* 2014). Reproductive effort has also been shown to increase with greater resource availability (Claisse *et al.* 2013). However, spatial gradients in environmental conditions, such as temperature, may modify both resource availability and reproductive rates (Durant *et al.* 2007). Elevated temperatures can positively influence the reproductive capacity of invertebrates, yet depressed reproductive rates may occur above and below windows of optional thermal tolerance (Bennett & Giese 1955). While food quality and availability are hypothesized to be more important than temperature in driving variation in reproductive output (Brockington & Clarke 2001), the relative importance of three

major driving factors – protection from fishing, resource availability, and temperature – on the demography of a marine species are virtually unknown.

A network of MPAs in the four Northern Channel Islands – situated along the southern California coast – offers an ideal setting for research focused on teasing apart the effects of environmental forcing on demographic variability in areas with and without fishing pressure. Eleven MPAs have been established around the 4 islands: the Anacapa Island State Marine Reserve (SMR) established in 1978 and ten established in 2003 (www.wildlife.ca.gov/Conservation/Marine/MPAs/Network/Southern-California; Hamilton *et al.* 2010). Previous studies within this region have documented changes in fish communities in response to the establishment of MPAs (Tetreault & Ambrose 2007; Hamilton *et al.* 2010) and the recovery of fished predatory species within many of the MPAs (Kay *et al.* 2012; Hamilton & Caselle 2014; Caselle *et al.* 2015).

The red sea urchin *Mesocentrotus franciscanus* (previously *Strongylocentrotus*) is heavily exploited as a commercial fishery across this biogeographically diverse region (Kalvass & Hendrix 1997; Kalvass & Rogers-Bennett 2004; Shears *et al.* 2012). While there is extensive knowledge of the basic ecology of southern California marine subtidal ecosystems (Tegner & Dayton 2000; Graham 2004; Foster & Schiel 2010; Shears *et al.* 2012), spatially-explicit patterns and drivers of variation in red sea urchin demographics remain poorly understood. Previous studies have reported greater size, biomass, and reproductive biomass of red sea urchins within a decades old reserve established in 1978 (Behrens & Lafferty 2004; Shears *et al.*

2012). Here, we explore how urchin populations respond to the broader network of MPAs that now span the region, following up to eight years of protection from fishing. Both urchin predators and the primary resource for urchins, the giant kelp (*Macrocystis pyrifera*, hereafter *kelp*) may increase in protected areas. Thus, the direct and indirect effects of MPAs on urchin populations may result in complex spatial patterns of urchin mortality and urchin grazing pressure, depending on the strength of species interactions throughout the food web (Behrens & Lafferty 2004; Lafferty 2004; Lafferty & Behrens 2005; Caselle *et al.* 2015; Foster *et al.* 2015).

The red sea urchin commercial fishery extracts over 5,000 metric tons (11 million pounds) of biomass annually (California Department of Fish and Wildlife [CDFW] catch data for 2004-13; www.wildlife.ca.gov). This multi-million dollar industry harvests urchins for their roe and targets individuals of high gonad quality. The fishery ranks within the top two coastal fisheries in California in annual landed weight, bringing in on average 7 million US dollars per year (2004-2013 prices paid to fishermen; CDFW [www.wildlife.ca.gov]). More than half of the state's landings and value (2002-2011) come from within the Northern Channel Islands, which represent only 5% of the state's coastline. Stocks were considered "fully exploited" after a peak in landings in the late 1980s and 20 years later, managers have provisionally classified the fishery as "over-fished" (Andrew *et al.* 2002; Kalvass & Rogers-Bennett 2004). Red sea urchin populations are doing poorly in some regions in southern California. For example, densities are believed to have further declined by approximately 50% between 2004 and 2008 around San Diego (Schroeter *et al.*

2009). No formal stock assessments have been performed since 2008. Thus to aid future management efforts, one goal of this study was to provide baseline data on red sea urchin demographics from the core region contributing to the fishery.

The coastal ecosystems of the Northern Channel Islands span a steep gradient in temperature (Fig. 1), productivity, and wave exposure, that results in dramatic biogeographic variation in community composition over a small spatial scale (Harms & Winant 1998; Blanchette *et al.* 2007; Hamilton *et al.* 2010). Rocky subtidal habitat is dominated by patches of dense stands of macroalgae largely made up of giant kelp, which supports a diverse fauna. Kelp stipe density is a strong indicator of drift kelp availability, an important sea urchin resource (Harrold & Reed 1985). Kelp is generally more abundant in the western than the eastern region of the islands, largely due to cooler temperatures, higher nutrients, and a reduced frequency of urchin barrens (Zimmerman & Kremer 1984; Behrens & Lafferty 2004; Cavanaugh *et al.* 2011; Palacios *et al.* 2013; Bell *et al.* 2015). Thus, resources for urchins are lower in the eastern part of our study area, and furthermore, the warmer temperatures there may exacerbate the negative effects of reduced resource availability on sea urchin reproductive output and mortality (Ebert *et al.* 1999; Tegner *et al.* 2001). Consequently, the western portion of the study region consistently experiences higher commercial red sea urchin landings than the eastern region (Shears *et al.* 2012, Teck *et al.* in preparation). However, there are areas of low kelp density in the cooler region and areas of high kelp density in the warmer region. Thus, we take advantage of the natural gradient in sea surface temperature and variation in kelp

density to decouple the relative importance of kelp density versus temperature variation as biological and physical drivers of red sea urchin demographics. While previous work found no significant spatial differences in size, density, biomass, and reproductive biomass of red sea urchins across this region (Shears *et al.* 2012), we improve (as discussed below) upon estimates of red sea urchin biomass and reproductive biomass and greatly increase the spatial resolution of sampling.

To explore the direct and interactive effects of protection from fishing, kelp density, and temperature in driving red sea urchin demography, we ask: (1) what are red sea urchin demographic patterns within and outside of MPAs across this region, and (2) what environmental factors may explain the variability in these patterns?

Methods

Biological surveys

To explore potential ecological factors associated with spatial variation in red sea urchin demographics, we conducted diver surveys of benthic kelp forest community structure throughout the four northern Channel Islands: Anacapa, Santa Cruz (SCI), Santa Rosa (SRI), and San Miguel Islands (SMI) (Fig. 1) during three northern-hemisphere summers (June-August in 2009 and 2011 and June-October in 2010). The sampling effort was a part of the Partnership for Interdisciplinary Studies of Coastal Oceans' (PISCO) benthic subtidal monitoring program (Hamilton *et al.* 2010; Caselle *et al.* 2015).

We sampled from two depth zones (6 and 13 m) at an average of 11 sites within MPAs and 13 unprotected areas (open to fishing) per year across the northern Channel Islands (n=30 unique sites across the three years). Although some sites were located within the same reef complex, sites were separated by at least 500 m. We considered each sampling event (n=143) as a separate replicate. Protected sites were located within seven MPAs (listed from west to east, Fig. 1): Harris Point State Marine Reserve (SMR), South Point SMR, Painted Cave State Marine Conservation Area (SMCA), Gull Island SMR, Scorpion SMR, Anacapa Island SMCA, and Anacapa Island SMR. Although recreational and commercial fishing of a limited number of species are allowed within the SMCAs, fishing for sea urchins is prohibited and thus SMCAs can be considered no-take marine reserves with respect to urchins. In comparison to unprotected areas, no-take marine reserves may have greater ecological differences than partially-protected conservation areas (Lester & Halpern 2008), but we found no consistent urchin demographic differences between SMCAs and SMRs (see Appendix A for selected ecological patterns across all seven MPAs). Thus, all SMRs and SMCAs were categorized together (hereafter, *MPAs*) for the purposes of our analyses.

Divers recorded densities of red sea urchins greater than 25 mm in test diameter along two 30 m × 2 m belt transects at each depth zone per site. To estimate sea urchin density, divers counted sea urchins within 10 m-segments along the belt transects. If divers counted 30 individuals before reaching the end of a 10-m segment, the length of the segment surveyed to that point was recorded, and densities

of the entire segment were estimated based on the number counted in the subsampled segment (i.e., variable area subsampling). Within these transects, we counted the number of kelp plants and the number of stipes per plant (for all stipes greater than 1 m in height) and summed the total stipes as our estimate of kelp density. For each site, density data for sea urchins and kelp were averaged across the two transects within the same depth zone.

Size-frequency data on red sea urchins were gathered through PISCO's program and the kelp forest monitoring program (KFMP) at the Channel Islands National Park (Shears *et al.* 2012; Kushner *et al.* 2013). We measured the first 150 urchins (comprehensively removing all urchins present in a given 2 m by 4 m swath until the desired number of urchins was reached) within a 50-100 m radius (depending on the density of urchins) of PISCO transects that had already been sampled. For sites (n=19) where PISCO did not collect size-frequency data, we used size-frequency data from nearby Channels Islands NPS KFMP sites (perpendicular to the fixed transects in a series of 2 m by 5-10 m swaths).

Sea urchin collections for individual-based and population-based analyses

We investigated red sea urchin demographic metrics that are both ecologically important and relevant to the fishery. To examine individual urchin characteristics, we haphazardly collected adult red sea urchins (n=15-20) per depth zone per site on each sampling date. We focused solely on adults greater than 50 mm (n=2216)

because red sea urchins reach sexual maturity between about 51 and 76 mm (Tegner 1989).

We examined two individual-based metrics of adult red sea urchin: *size* (test diameter) and *gonadosomatic index* (GSI – a strong metric of reproductive stage and value to the fishery – Unuma 2002; Teck *et al.* in preparation):

GSI = gonad wet weight / total wet weight (1)

(i.e., the fraction of the organism mass that is gonad). We examined GSI separately for males and females.

To understand detailed regional variability in population-based characteristics of red sea urchins, we examined the patterns in: *density* (juvenile and adult individuals >25 mm per m^2), *adult biomass*, and *reproductive biomass* as a proxy for potential reproductive output. Biomass is a useful metric for assessing the population in both ecological and management terms. We examined adult biomass, since the fishery is based on harvesting adults (see Appendix B for information on juveniles and total biomass). We first estimated the proportion of adult red sea urchins (>50 mm) per site for each year using size-frequency collections from PISCO or KFMP. To estimate adult red sea urchin density (for the adult biomass metric), we multiplied the proportion of adult red sea urchins by the density (individuals >25 mm) per depth zone per site. Adult biomass per unit area within a site was estimated as:

adult biomass = adult density * mean adult whole weight (g) (2).

Reproductive biomass per unit area within a site was estimated as:

reproductive biomass = adult density * mean gonad weight (g) (3).

Previous estimates of biomass and reproductive biomass within this region were based on average weight and gonad measurements from a single site (Shears *et al.* 2012), whereas we calculated site-specific weights.

Environmental data

To examine the effect of spatial variation in temperature on red sea urchin demographics, we averaged satellite sea surface temperature (SST) records at each site from the previous year from the MODIS Terra and Aqua sensors (spg.ucsd.edu/Satellite_data/California_Current) at a 1-km spatial resolution (the closest pixel to each site). The data were daily images that were averaged into 15-day means (there is often cloud cover on any one daily image) and then averaged across the prior year to each site's sampling date.

Data analyses

First, we described the geographic patterns of sea urchin demographic variables. Since the islands are oriented west to east, the environmental gradient in

temperature, productivity, and wave exposure is strongly correlated with longitude (r=0.96, P<0.0001) (Fig. 1). Thus, longitude is a convenient proxy for multiple interrelated environmental forcing variables. We used general linear models (GLMs) to examine how the sea urchin demographic variables (Table 1) changed as a function of protection from fishing, longitude, depth, and among years. We initially executed full-factorial designs for each model and then sequentially removed all non-significant interaction terms.

Second, we examined the relative importance and interactions among three predictor variables (Table 1: protection from fishing [MPA versus unprotected area], mean kelp density, and mean sea surface temperature [over the previous year]) in driving red sea urchin demographics. We performed full-factorial GLMs for each of our five red sea urchin response variables (Table 1). All models were performed using JMP® 12.0.0, SAS Institute Inc. Transformations for predictor variables were performed to normalize the residuals of the models and are shown in Table 1. Since SMI contains a red sea urchin barren unique to the entire study region, we explored excluding sites within this island to see if drivers were different.

Results

Spatial and temporal variation in red sea urchin demography

Individual-based metrics: GSI and adult test diameter

There were no consistent spatial differences in GSI as a function of gender and thus males and females were pooled for further analyses (Appendix C). Sea urchins

had higher GSI and were larger in the west (Table 2; Fig. 2; Appendix D). On average red sea urchins had 28% higher GSI and were 14% larger at the two western islands than at the two eastern islands. Gonadosomatic index was also greater at unprotected than protected sites but only in the west, whereas there were no differences among protected and unprotected sites in the East. The lack of a consistent regional pattern within MPAs was largely driven by the very low GSI levels at the SMI MPA. There were no year-to-year differences in GSI.

Adult test diameter (TD) was on average 6% greater (5.2 mm) within MPAs across the region than at unprotected sites (Table 2; Fig. 2). In addition, there was a significant interaction between the east-west gradient (longitude) and depth; adult red sea urchins in the west were larger at deeper sites, but there was no clear relationship with adult size and depth in the east. Finally, adult red sea urchins were significantly larger in 2009 by on average 11 mm (88 mm) than in 2011 (77 mm), and were of intermediate size in 2010 (85 mm).

Population-based metrics: density, adult biomass, and reproductive biomass

Red sea urchin densities were highly variable across the region. There were significant two-way interactions between the east-west gradient (longitude) and year, protection from fishing, and depth (Table 2; Fig. 3). In 2009, densities were greater in the east. Generally, unprotected sites were no different in red sea urchin density across the east-west gradient, but within MPA sites, red sea urchin densities were

greater in the west. In addition, within the west, densities were negatively related to depth.

Both adult red sea urchin biomass and reproductive biomass were significantly greater within MPA sites than unprotected sites (by 16% and 23%, respectively) and within shallower depth zones (Table 2; Fig. 3). Reproductive biomass also was significantly greater in the west than the east (on average red sea urchins had 9% higher reproductive biomass at the two western islands than at the two eastern islands) (Table 2; Fig. 3). There were no year-to-year differences in biomass and reproductive biomass.

Drivers of red sea urchin demography

Individual-based metrics: GSI and adult test diameter

Kelp density was the strongest predictor of both GSI and size among sites (Table 3); sites with more kelp tended to have red sea urchins with greater GSI and of larger size (Fig. 4a and b). The positive relationship between kelp density and size was even stronger within MPAs than within unprotected sites (there was a significant interaction between protection from fishing and kelp density) (Table 3; Fig. 4). The only other significant predictor of individual urchin characteristics was SST. Both red sea urchin size and GSI declined with increasing SST, following the longitudinal patterns described above.

Population-based metrics: density, adult biomass and reproductive biomass

Red sea urchin density varied significantly across the islands, however the spatial patterns were complex due to a significant 3-way interaction between three factors: protection from fishing (MPA versus unprotected area), kelp density, and SST (Table 3; Fig. 4c). Kelp density was negatively related to red sea urchin density, but this relationship only occurred within protected areas in the western, cooler region (Fig. 4c).

Protection from fishing was the strongest individual predictor of urchin adult biomass (Table 3; Fig. 4d), with 16% higher biomass within MPAs. In addition, there was a significant interaction between kelp density and SST, where adult biomass was positively associated with kelp density in the warmer (eastern) region and negatively associated with kelp density within the cooler (western) region (Fig. 4d). The western region also receives the greatest fishing pressure (Shears *et al.* 2012, Teck *et al.* in preparation).

Overall, reproductive biomass was 23% greater within MPAs than in unprotected areas (Table 3; Fig. 3, 4e). In general, reproductive biomass was positively related to kelp density and negatively related to SST. However, these two drivers interacted — there were slightly higher levels of reproductive biomass in areas with higher densities of kelp within the warmer and less fished eastern region (Fig. 4e). The opposite pattern occurred in the cooler (western) region (Fig. 4e), where reproductive biomass declined with kelp density, similar to the pattern for adult biomass.

Drivers of sea urchin demography excluding sites within SMI

If we exclude SMI from these analyses, kelp and SST are the only significant drivers of variation in red sea urchin adult density with no significant interactions. In addition, without sites in SMI, SST is no longer an important predictor of variation in GSI or reproductive biomass but otherwise results are similar. Finally, drivers of TD and biomass are statistically similar with the exclusion of SMI (Appendix D, Table D2).

Discussion

Similar to studies from South Africa, Chile, New Zealand, the Mediterranean, and elsewhere around the globe (Babcock *et al.* 2010; Ling *et al.* 2015), we also found that protection from fishing, kelp density, and temperature interact to explain the complexity of sea urchin demographics across the Channel Islands (*see* Table 4 *for a summary of the key results*). Although the majority of the MPAs within the region had only been designated six years prior to this beginning of this study, we detected significant differences in red sea urchin demographics between MPA and unprotected sites. Kelp density was the most important direct driver of red sea urchin GSI and adult size and this factor was included in all the significant interaction terms in statistical models investigating the effects of protection from fishing and environmental forcing on red sea urchin population-based metrics. In addition, as described below, we found several prominent regional differences in sea urchin demographics, which help explain the regional differences in fishing pressure and fishermen behavior across the northern Channel Islands (e.g., Shears *et al.* 2012).

While previous research reported no significant spatial differences across this same region in red sea urchin reproductive biomass (Shears *et al.* 2012), we detected large spatial variation in reproductive characteristics. One potential explanation for this discrepancy is that Shears and colleagues (2012) calculated reproductive biomass from average weight and gonad measurements from a single site and applied those relationships broadly to data collected on surveys in other locations, whereas we calculated site-specific demographic variables. If the relationship between urchin size and reproductive condition (GSI) varies from place to place in response to environmental forcing (as our results indicate), assumptions of spatial invariance may result in errors when applied over large geographic scales.

Despite higher fishing mortality rates in the west (Shears *et al.* 2012; Teck *et al.* in preparation), red sea urchins were still larger and had greater reproductive potential in the western (colder) region. This result is partially due to the enhanced primary productivity and greater kelp resource availability in the western region (Shears *et al.* 2012; Appendix E), and for many species including red sea urchins more food availability can result in higher reproduction (Claisse *et al.* 2013). We not only detected greater total reproductive biomass in western sites but also greater size-specific individual reproductive potential (GSI) in this region. Both reproductive measures were higher in the west, also partially due to the higher frequency of larger red sea urchins in this region. While some invertebrates typically senesce at a certain age and size, long-lived species may not show reductions in reproductive capacity;

larger sea urchins typically have higher reproductive output and higher GSI than smaller conspecifics (Gonor 1972; Ebert 2008).

Furthermore, GSI was marginally significantly higher within unprotected western (colder) sites where kelp densities were significantly higher and purple sea urchin (*Strongylocentrotus purpuratus*) densities were lower (Appendix E). Purple sea urchins are prime space and resource competitors with red sea urchins (Dewees 2003; Rogers-Bennett 2007). More resource availability in the western region likely supports higher per-capita gonad growth; larger and heavier sea urchins found at western islands are consistent with this hypothesis (Ebert 1968). In addition, the significant decline in many reproductive measures between MPA and unprotected locations within the western (colder) region is partially due to (1) a unique red urchin barren that formed at SMI (Harris Point) in years prior to the implementation of the MPA network (Kushner *et al.* 2013; Appendix A) and (2) the heavier fishing pressure outside of this MPA (Teck *et al.* in preparation) that alleviates resource competition for the remaining urchins.

Depth was an important indicator of variability in red sea urchin density, adult biomass, and reproductive biomass. Shallower areas (6 m) had higher levels of all of the red sea urchin population-based metrics than deeper areas (13 m). Shallower areas (5-8 m) are associated with greater accumulation of drift kelp (Rogers-Bennett *et al.* 1995; Basch & Tegner 2007), a primary resource for sea urchins, than deeper areas (14-23 m). In addition, standing kelp is a good indicator of drift kelp

availability (Harrold & Reed 1985), and on many California rocky reefs kelp density is higher within shallower areas (Appendix E; Young *et al.* in press).

Evidence from this study can help to explain the presence of a strong gradient in fishing pressure across the Channel Islands, with significantly higher landings in the west versus the east (Shears *et al.* 2012; Teck *et al.* in preparation). Partly due to the higher probability of finding larger red sea urchins in the west, the western region has been among the most productive regions for the commercial sea urchin fishery in recent decades (CDFW data [www.wildlife.ca.gov]). In addition, higher GSI is an indicator of superior gonad quality, which translates to higher prices (Kalvass & Hendrix 1997; Unuma 2002; Teck *et al.* in preparation). We found that red sea urchins were larger with higher quality gonads in the western region even though these sites experience consistently higher commercial fishing pressure (Teck *et al.* in preparation.).

Previous research has indicated that red sea urchin size structure and reproductive potential has benefitted from protection in the older marine reserve at Anacapa Island, which was established in 1978 (Tuya, Soboil & Kido 2000; Behrens & Lafferty 2004; Shears *et al.* 2012). (see Appendix F; Behrens & Lafferty 2004; Shears et al. 2012).The newer reserves of the Channel Islands network (established in 2003) are already showing similar trends in conservation benefits. Adult red sea urchins were significantly larger (by 5.2 mm), had greater biomass, and greater reproductive biomass within MPA sites. Our findings corroborate previous research and catch data (CDFW) that show fishermen are removing large amounts of biomass

outside of MPAs and altering the size distributions by focusing harvest on sea urchins above the minimum size limit of 83 mm (Behrens & Lafferty 2004).

In summary, protection from fishing was an important driver of red sea urchin density, adult size, biomass, and reproductive biomass. All red sea urchin demographic metrics were higher within protected areas versus unprotected areas. Protection from fishing was the most important predictor of population levels of adult biomass, underlining effects of MPAs and fishing within this region. We found that kelp density was the most important driver of individual-based red sea urchin metrics: GSI and adult size. In addition, larger adult red sea urchins were associated with cooler temperatures in the west but were more strongly determined by regional differences in kelp density than temperature.

Sea surface temperature (SST) alone was not the most important predictor of any of the sea urchin metrics. However, there were significant interactions between SST and other predictors for all of our red sea urchin population-based metrics. In particular, kelp density was positively related to red sea urchin adult biomass and reproductive biomass but only within the warmer (eastern) region. We thus found that regardless of temperature, there were significant differences in red sea urchin demographics across MPA and unprotected areas in the entire northern Channel Islands region (farthest right column of Table 4). Similarly, regardless of the level of protection from fishing, there were regional differences associated with variation in temperature (bottom row of Table 4). Through these investigations, we have been able to estimate the relative importance of these regional temperature differences,

protection from fishing, and availability of resource on demographic variability in a fished species.

Implications

Species targeted by fishing activities frequently recover in density, size, and biomass inside well-designed marine protected areas (MPAs) (Lester *et al.* 2009; Babcock *et al.* 2010; Ling & Johnson 2012; Coleman *et al.* 2015; Munguía-Vega *et al.* 2015). As we have shown here, the corresponding higher reproductive potential within MPAs can be a key benefit to species protection (Allison *et al.* 1998; Gell & Roberts 2003; Tetreault & Ambrose 2007) and may contribute to enhancing fisheries outside MPAs (Gaines *et al.* 2010; Rossetto *et al.* 2015). Despite this, in some situations the simple prediction that more protection leads to greater abundance, larger size, and greater reproductive potential of a fished species is not realized; other species may compensate for the reduced mortality from fishing via predation (Allison *et al.* 2003; Shears *et al.* 2012).

Both of our statistical models that tested (1) the importance of geographic proxies for environmental variables (i.e., longitude) or (2) specific environmental forcing variables (temperature and kelp abundance) on red sea urchin demographics, indicated that larger sizes, greater biomass, and reproductive potential of red urchins occurred within MPAs versus unprotected areas. Although urchin predators have recovered within protected areas of this region (Kay *et al.* 2012; Hamilton & Caselle 2014; Caselle *et al.* 2015), there were significant population-level responses by

urchins to the elimination of fishing pressure. It remains to be seen whether these patterns will change as the predator populations continue to grow or individual predators achieve larger sizes. When fished predators increase within protected areas, such as in southern California, Australia, New Zealand, the Caribbean, the Mediterranean, and elsewhere, they can drive classic trophic cascades, resulting in lower densities of herbivores (Sala 1997; Babcock *et al.* 1999, 2010; McClanahan 2000; Shears & Babcock 2002, 2003; Micheli *et al.* 2005; Pederson & Johnson 2006; Guidetti 2006; McClanahan *et al.* 2007; Barrett *et al.* 2009; Harborne *et al.* 2009; Salomon *et al.* 2010; Leleu *et al.* 2012; Berriman *et al.* 2015; Ling *et al.* 2015) even when they are targeted by fishing (Shears *et al.* 2012; Nichols *et al.* 2015). Thus, protection from fishing across all trophic levels may, in some cases, result in lower herbivore density and consequently lower recruitment. However, the older reserve at Anacapa Island suggests that red sea urchins within MPAs may remain at population levels that are well above unprotected sites even in the long term, and the net gains from reduced fishing mortality are not entirely offset by increases in natural mortality. Thus, future research could address the relative roles of predation (by humans and other predators) and competition (mainly from the purple sea urchin, *Strongylocentrotus purpuratus*) as drivers of red sea urchin population dynamics.

While predation pressure is an important structuring force for herbivores and their algal prey in nearshore coastal waters (Hamilton & Caselle 2014; Ling *et al.* 2015), our results underscore the significant impacts from humans as predators (Castilla 1999; Pinnegar *et al.* 2000; Darimont *et al.* 2009; Ling *et al.* 2009) on

herbivores that are themselves an important ecological engineer. Our results show that the alleviation of human predation through marine protected areas can benefit fished herbivores, but herbivore demographics are also tightly linked with macroalgal dynamics embedded in a complex thermal regime.

Acknowledgements

This study utilized data collected by the Partnership for Interdisciplinary Studies of Coastal Oceans, a long-term ecological consortium funded by the David and Lucile Packard Foundation and the Gordon and Betty Moore Foundation. This research would not have been possible without the tireless efforts of the PISCO scientific dive team, in particular Katie Davis and Avrey Parsons-Field. Deep thank yous to L. Anderson, J. Benson, P. Carlson, L. Hesla, C. Lantz, D. Macaskill, E. Nickisch, D. Simpson, A. Soccodato, N. Spindel, S. Toyama, and S. Windell, who assisted with fieldwork, and M. Adams, A. Alger, G. Alongi, K. Asanion, M. Bogeberg, E. Casas, J. Conley, D. Cooper, C. Fitzgerald, S. Ginther, M. Hunt, W. Meinhold, S. Meinhold, A. Poppenwimer, A. Quintana, S. Rathbone, T. Rogier, J. Roh, C. Scianna, R. Shen, T. Shultz, A. Stroud, K. Treiberg, O. Turnross, and A. Wong, all of whom assisted with labwork; Jeremy Claisse for summarizing the satellite sea surface temperature data; Jim Carlton and Bob Warner for reviewing earlier versions of this manuscript; and Dave Kushner with the Channel Islands National Park Service Kelp Forest Monitoring Program for providing red sea urchin size structure data.

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Tables

Table 1. List of all variables, abbreviations, and their transformations for statistical models, if any.

Variable	Variable abbreviation	Transformation
Response variables:		
Mean red sea urchin (SU) gonadosomatic index	GSI	none
Mean adult red SU test diameter	TD	none
Mean red SU density	density	ln (x+1)
Mean adult red SU biomass	biomass	ln (x+1)
Mean red SU reproductive biomass	reprod	ln (x+1)
Predictor variables:		
Protection from fishing (MPA versus unprotected area)	MPA	binary variable
Mean kelp density	kelp	ln (x+1)
Mean sea surface temperature (over previous year)	SST	none

Table 2. General linear models examining spatial variability (year, longitude, protection from fishing, and depth) across individual-based and population-based response variables: red sea urchin gonadosomatic index (GSI), adult size (TD), density, adult biomass, and reproductive biomass: (a) overall model R^2, F-ratio, DF, and *P*-values and (b) effect tests. All non-significant interaction terms were sequentially removed.

(a)

	individual metrics		population metrics		
Response Variable	GSI	TD	density	biomass	reprod
R^2	0.120	0.285	0.324	0.142	0.167
$F\text{-ratio}_{DF}$	$F_{6,142}$	$F_{6,142}$	$F_{9,142}$	$F_{5,142}$	$F_{5,142}$
	3.10	9.02	7.09	4.54	5.48
P	0.007	<0.0001	<0.0001	0.0007	0.0001

(b)

		individual metrics									population metrics								
		GSI			TD			density			biomass			reprod		
Source	DF	F	*P*		F	*P*		F	*P*		F	*P*		F	*P*	
year	2	0.38	0.683		7.18	0.0011	**	0.45	0.6365		0.08	0.9222		0.16	0.8504	
long	1	9.99	0.0019	**	25.04	<0.0001	***	0.26	0.608		1.31	0.2543		6.82	0.01	*
year*long	2							5.78	0.0039	**						
MPA	1	0.03	0.8619		9.70	0.0022	**	4.70	0.0319	*‡	13.20	0.0004	***	11.74	0.0008	***
long*MPA	1	3.89	0.0507	†				7.54	0.0069	**						
depth	1	0.67	0.414		2.28	0.1335		31.49	<0.0001	***	9.25	0.0028	**	12.46	0.0006	***
long*depth	1				6.37	0.0128	*‡	4.84	0.0295	*						

† marginally significant p-value
‡ p-values were >0.05 when all interaction terms remained in the analysis
*p≤0.05
**p≤0.01
***p≤0.001

Table 3. General linear models examining spatial drivers (protection from fishing, kelp density, SST, and interactions) across individual-based and population-based response variables: red sea urchin GSI, adult TD, density, adult biomass, reproductive biomass: (a) overall model R^2, F-ratio, DF, and *P*-values and (b) effect tests.

(a)

		individual metrics		population metrics		
Response Variable		GSI	TD	density	biomass	reprod
	R^2	0.459	0.430	0.262	0.163	0.259
F-ratio$_{7,142}$		16.35	14.53	6.84	3.75	6.73
	P	<0.0001	<0.0001	<0.0001	0.001	<0.0001

(b)

		individual metrics				population metrics					
		GSI		TD		density		biomass		reprod	
Source	DF	F	*P*	F	*P*	F	*P*	F	*P*	F	*P*
MPA	1	0.1	0.7813	10.1	0.0018 **	4.2	0.0415 *	10.8	0.0013 **	10.8	0.0013 **
kelp	1	82.7	<0.0001 ***	55.8	<0.0001 ***	19.6	<0.0001 ***	0.0	0.8458	7.1	0.0085 **
MPA*kelp	1	1.7	0.1993	4.5	0.0002 **	1.8	0.1816	0.2	0.6236	1.0	0.3226
SST	1	5.3	0.0229 *	13.7	0.0003 **	0.5	0.4776	1.2	0.2668	4.2	0.0417 *
MPA *SST	1	1.1	0.3049	0.6	0.4218	2.7	0.0996	0.0	0.8578	0.2	0.6951
kelp*SST	1	0.3	0.5792	0.6	0.4548	4.6	0.0343 *	8.3	0.0047 **	10.9	0.0012 **
MPA*kelp*SST	1	1.2	0.2798	0.4	0.5546	18.0	<0.0001 ***	2.2	0.1398	2.9	0.0887

*p≤0.05
**p≤0.01
***p≤0.001

Table 4. Red sea urchin metrics across western (colder SST) and eastern (warmer SST) regions within the northern Channel Islands and MPAs *versus* unprotected areas (2009-2011). Unless otherwise noted, metrics refer to mean red sea urchin values.

REGION STATUS	WESTERN REGION (colder)	EASTERN REGION (warmer)	ENTIRE REGION (colder or warmer)
MPA	** densities higher (largely due to sites within Harris point SMR, SMI) *** urchin density *negatively related* with kelp density (largely due to sites within Harris point SMR, SMI)		** adult size larger ** adult biomass higher ** reproductive biomass higher ** adult size *positively related* with kelp density
UNPROTECTED	† GSI marginally higher (largely due to sites within Harris point SMR, SMI)		
MPA or UNPROTECTED	* adults larger and * densities lower at deeper sites ** GSI higher * reproductive biomass higher ** adult biomass and reproductive biomass *negatively related* with kelp density	** densities higher in 2009 ** adult biomass and reproductive biomass *positively related* with kelp density	** adult biomass and *** adult reproductive biomass higher at shallower sites ** adult size in 2009 larger than in 2011 (intermediate in 2010) *** GSI *positively related* with kelp density * GSI and ** adult size *negatively related* with SST

† marginally significant p-value; *p≤0.05; **p≤0.01; ***p≤0.001

Figures

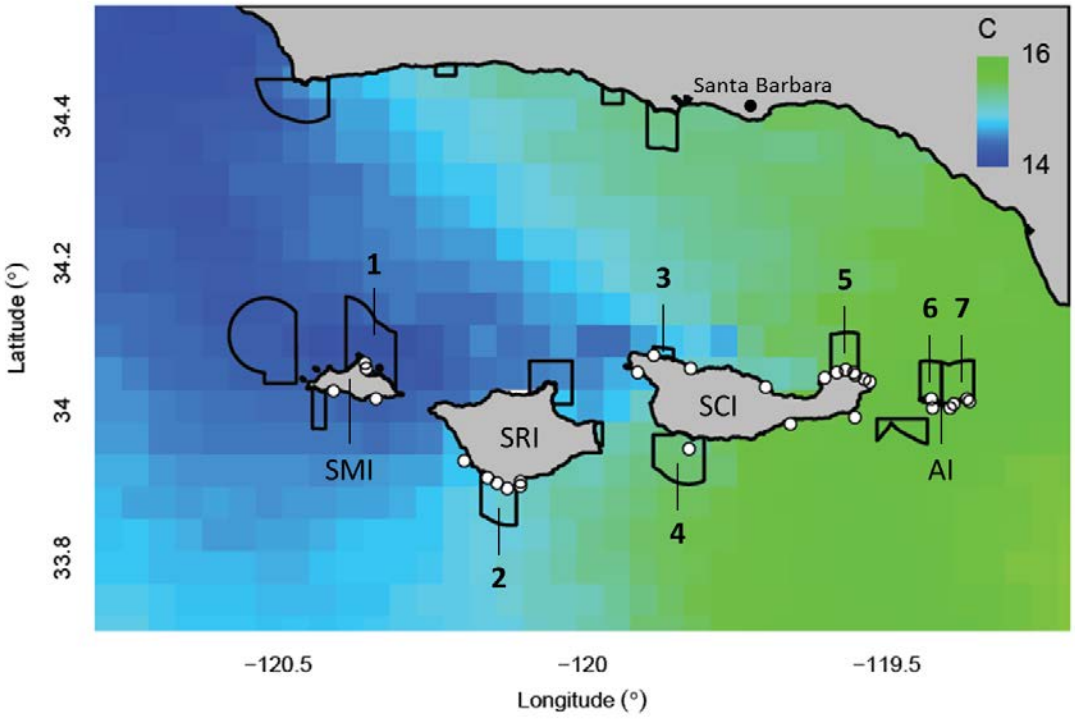

Figure 1. Map of the Santa Barbara Channel and northern Channel Islands with sites (white dots) and mean long-term satellite sea surface temperatures (SST) represented by colors from blue to green (25-year average Advanced Very High Resolution Radiometer data from 1985-2009). All marine protected areas (MPAs) are outlined in black. The sites examined in this study are within seven MPAs (1) Harris Point State Marine Reserve (SMR), (2) South Point SMR, (3) Painted Cave State Marine Conservation Area (SMCA), (4) Gull Island SMR, (5) Scorpion SMR, (6) Anacapa Island SMCA, and (7) Anacapa Island SMR. Islands from west to east are shown: San Miguel Island (SMI), Santa Rosa Island (SRI), Santa Cruz Island (SCI), and Anacapa Island (AI). Twenty-five-year and one-year averages of SST are highly correlated with longitude (r=0.949, P<0.0001; r=0.959, P<0.0001, respectively).

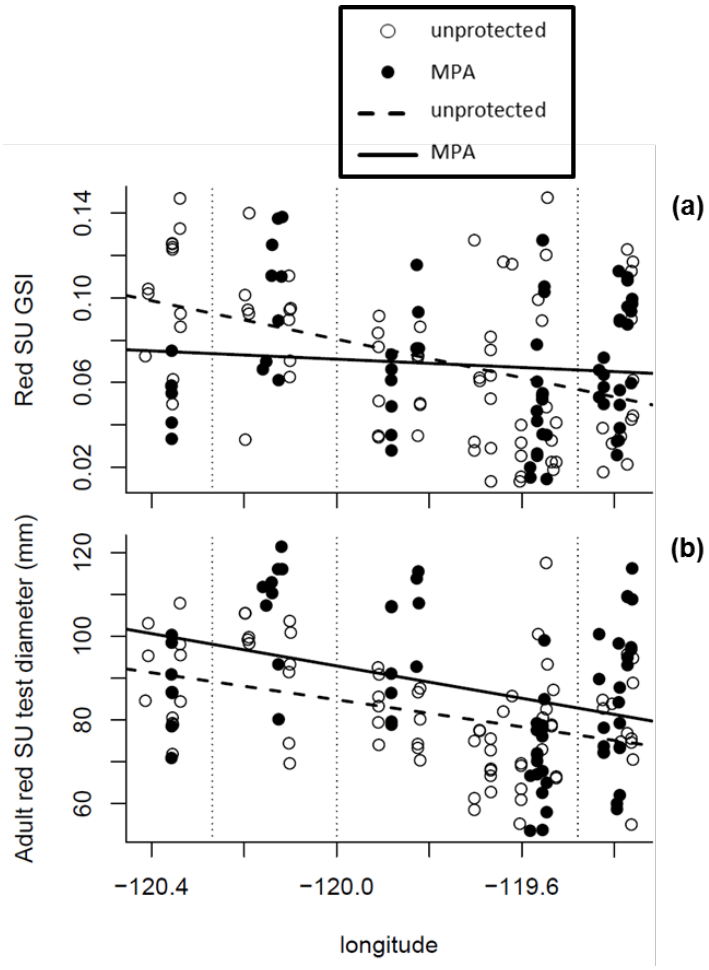

Figure 2. Mean red sea urchin (SU) (a) gonadosomatic index (GSI) and (b) adult red SU test diameter (TD) per site per year across longitude from west to east (left to right) and grouped across MPA and unprotected areas. Vertical dotted lines separate the islands: San Miguel, Santa Rosa, Santa Cruz, and Anacapa Islands. Lines show linear regressions across longitude and between MPA and unprotected areas (GSI: R^2=0.11, $F_{3,142}$=5.92, P=0.0008; TD: R^2=0.16, $F_{3,142}$=9.08, P<0.0001).

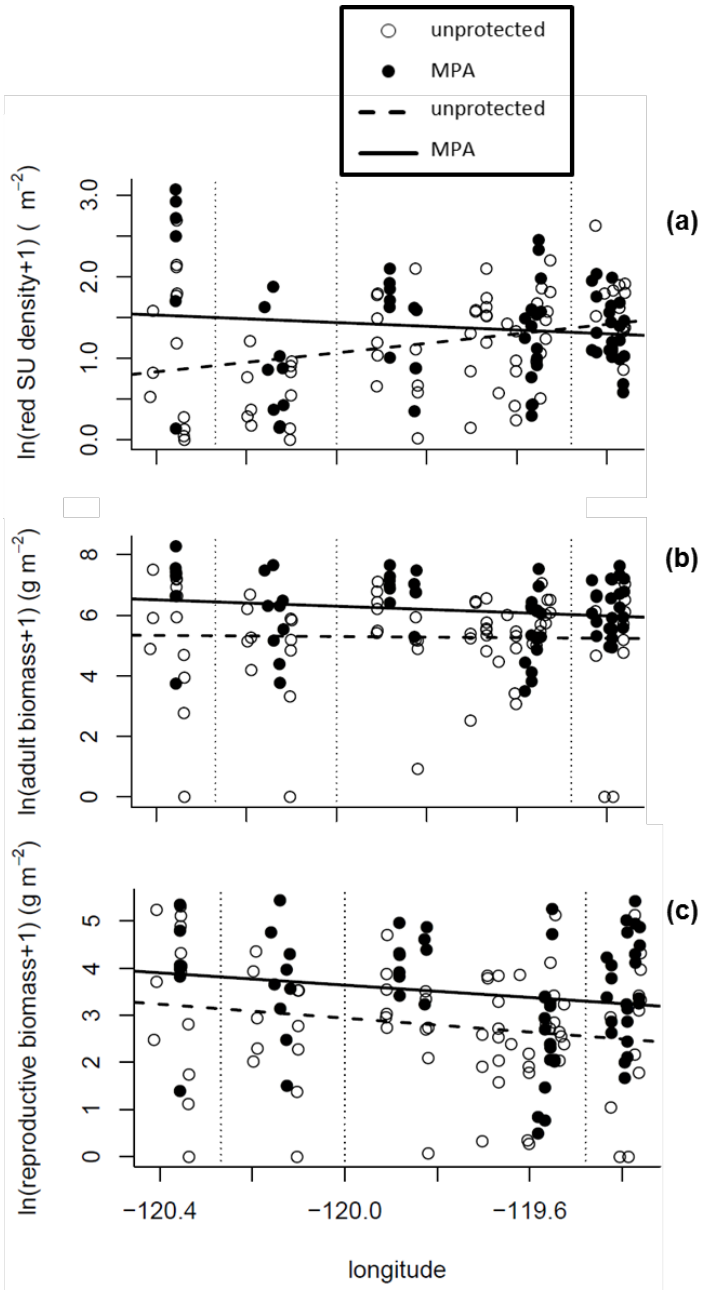

Figure 3. Mean red sea urchin (SU) (a) density, (b) adult biomass, and (c) reproductive biomass (showing log-transformed values) across longitude from west to east (left to right) and grouped by MPA and unprotected areas. Vertical dotted lines separate the islands: San Miguel, Santa Rosa, Santa Cruz, and Anacapa Islands. Lines show linear regressions across longitude and between MPA and unprotected areas (density: R^2=0.08, $F_{3,142}$=3.80, *P*=0.0118; adult biomass: R^2=0.09, $F_{3,142}$=4.33, *P*=0.0060; reproductive biomass: R^2=0.09, $F_{3,142}$=4.56, *P*=0.0044).

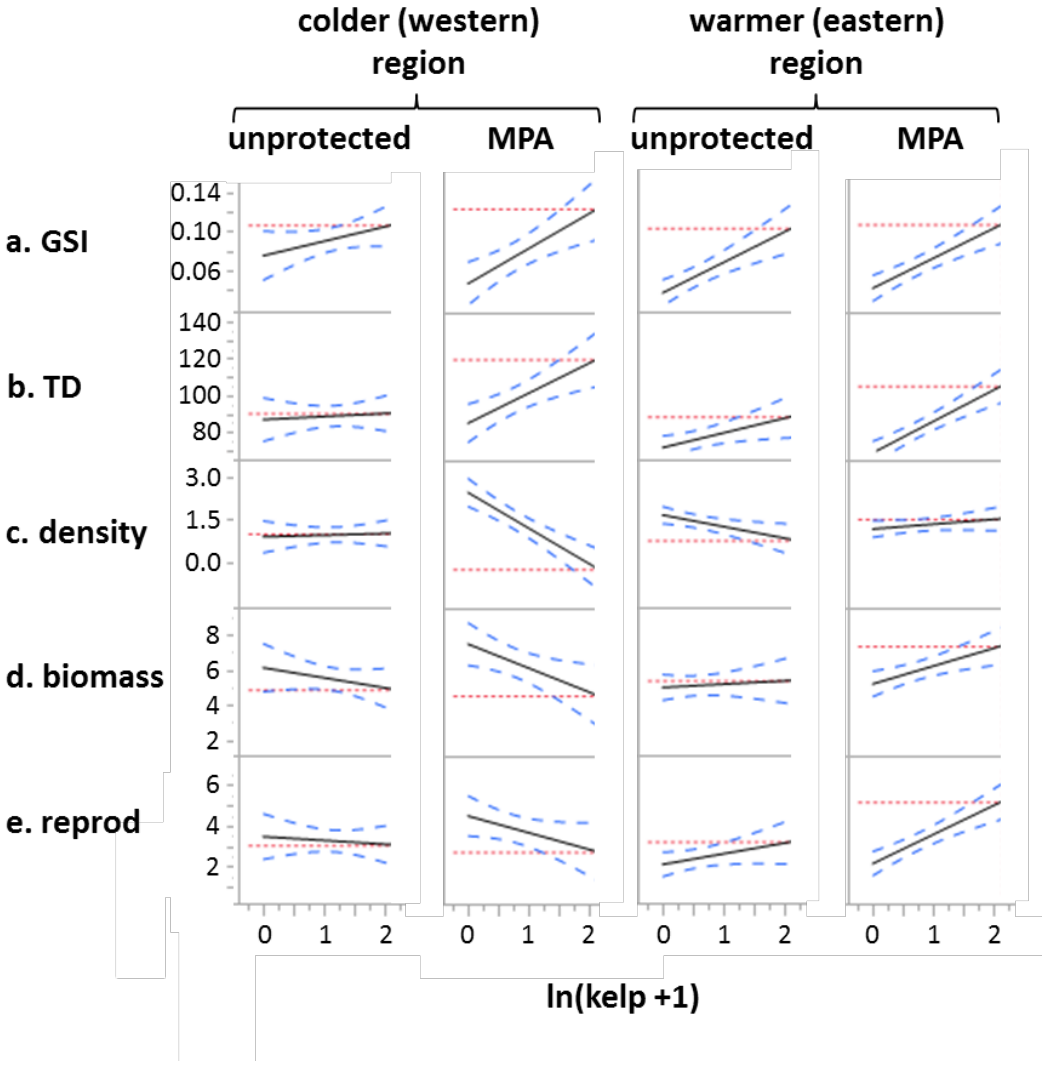

Figure 4. Results from the GLMs examining spatial drivers (protection from fishing, kelp density, sea surface temperature [SST], and interactions) on urchin demographics. Figures depict the relationship between kelp density (m^{-2}) and each sea urchin demographic metric: (a) gonadosomatic index (GSI) and (b) adult test diameter (TD) (mm), (c) density (m^{-2}), (d) adult biomass (above 51 mm) (g m^{-2}), (e) reproductive biomass (g m^{-2}) (reprod). The black lines show the predicted value of each metric across a range of kelp density within the western region (left two columns) and the eastern region (right two columns) across both unprotected and MPA sites. The blue dashed lines show the 95% confidence interval for the predicted values. Red dotted lines show the predicted value of each sea urchin demographic metric (horizontal lines) at the highest kelp level (vertical lines).

Appendix A
Variation across seven MPAs with a description of regulations

Except for the two Marine Conservation Areas (SMCAs), all other MPAs are designated as State Marine Reserves, where the "take of all living marine resources is prohibited" (CDFW website). At the Painted Cave State Marine Conservation Area (SMCA), the "take of all living marine resources is prohibited except for the recreational take of spiny lobster and pelagic finfish[1]." At the Anacapa Island SMCA (north coast of Anacapa Island)[2] the "take of all living marine resources is prohibited except for the recreational take of spiny lobster and pelagic finfish and the commercial take of spiny lobster."

ANOVAS across sites within the seven MPAs for mean red sea urchin (SU) gonadosomatic index (GSI), adult red SU test diameter, density, juvenile biomass (25-50 mm), adult biomass (above 51 mm), total biomass, reproductive biomass (reprod), mean kelp density, and purple sea urchin density are presented below (Table A1, Figure A1). We expected to see greater sea urchin density (both red and purple sea urchins *Strongylocentrotus purpuratus*) and greater red sea urchin adult biomass and lower kelp density within SMCAs versus SMRs due to fewer lobsters from fishing for lobsters (Behrens & Lafferty 2004; Lafferty 2004; Lafferty & Behrens 2005; Caselle *et al.* 2015; Foster *et al.* 2015). We also predicted that red sea urchin density and adult biomass would be lowest and kelp density highest at the old SMR in Anacapa since predator populations have had the longest time to recover in comparison to other SMRs. However, there may be spatial differences, for instance north versus south side of the islands have different temperature and ocean circulation regimes.

In addition, there is a historical presence of high densities of adult red sea urchins in the western Harris Point State Marine Reserve (SMI), which existed prior to reserve establishment (1985-2003 data from Shears *et al.* 2012; Kushner *et al.* 2013). Persistence of this red "sea urchin barren" may be explained by a lack of fishing within this MPA, the slow recovery of urchin predators of sufficient size to attack adult urchins, and adult sea urchins providing protection from predation on juveniles (<40 mm) with their spine canopies (Tegner & Dayton 1977, 1981; Breen *et al.* 1985; Zhang *et al.* 2011). In addition, predators may prefer consuming sea urchins living among kelp beds rather than in barren areas (Eurich *et al.* 2014).

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[1]"Pelagic finfish (CCR Title 14, Section 632(a)(3)), as defined for purposes of MPA regulations, are a subset of finfish defined as: northern anchovy (*Engraulis mordax*), barracudas (*Sphyraena* spp.), billfishes[3] (family Istiophoridae), dolphinfish (*Coryphaena hippurus*), Pacific herring (*Clupea pallasii*), jack mackerel (*Trachurus symmetricus*), Pacific mackerel (*Scomber japonicus*), salmon (*Oncorhynchus* spp.), Pacific sardine (*Sardinops sagax*), blue shark (*Prionace glauca*), salmon shark (*Lamna ditropis*), shortfin mako shark (*Isurus oxyrinchus*), thresher sharks (*Alopias* spp.), swordfish (*Xiphias gladius*), tunas (family Scombridae), including Pacific bonito (*Sarda chiliensis*), and yellowtail (*Seriola lalandi*)."

[2]"The state conservation area and federal conservation area share identical regulations. For complete state boundaries and rules, see California Code of Regulations Title 14, Section 632. For federal MPAs see Code of Federal Regulations, Federal Register 15 Part 922 and 50 CFR Part 660."

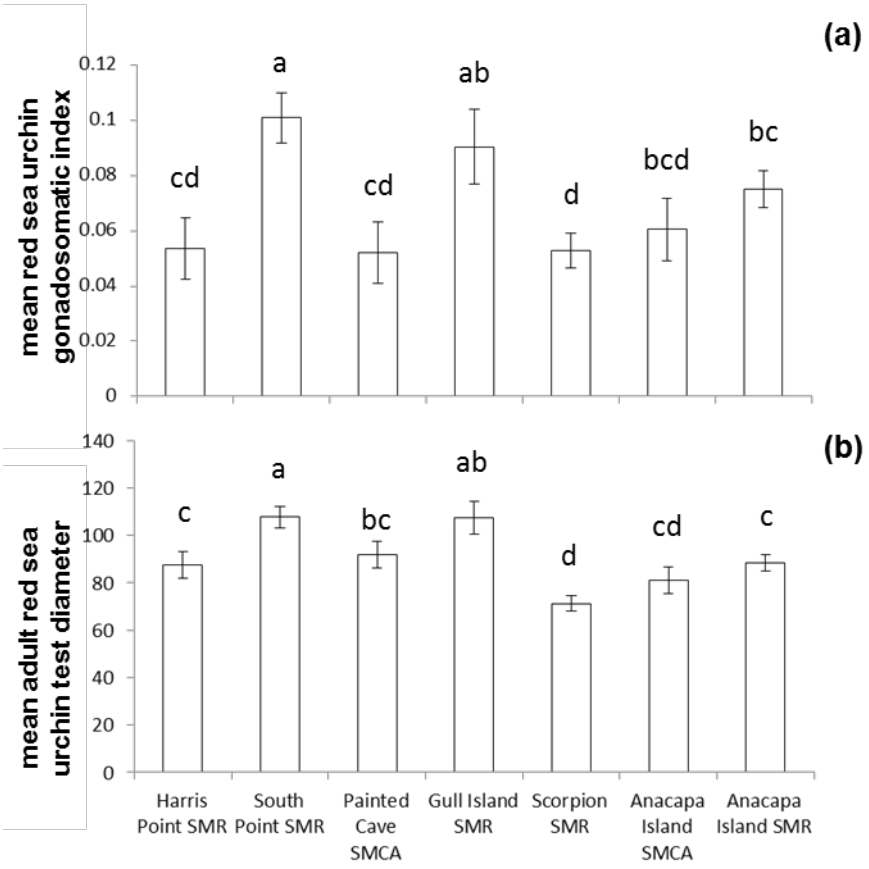
[3]"Marlin is not allowed for commercial take."

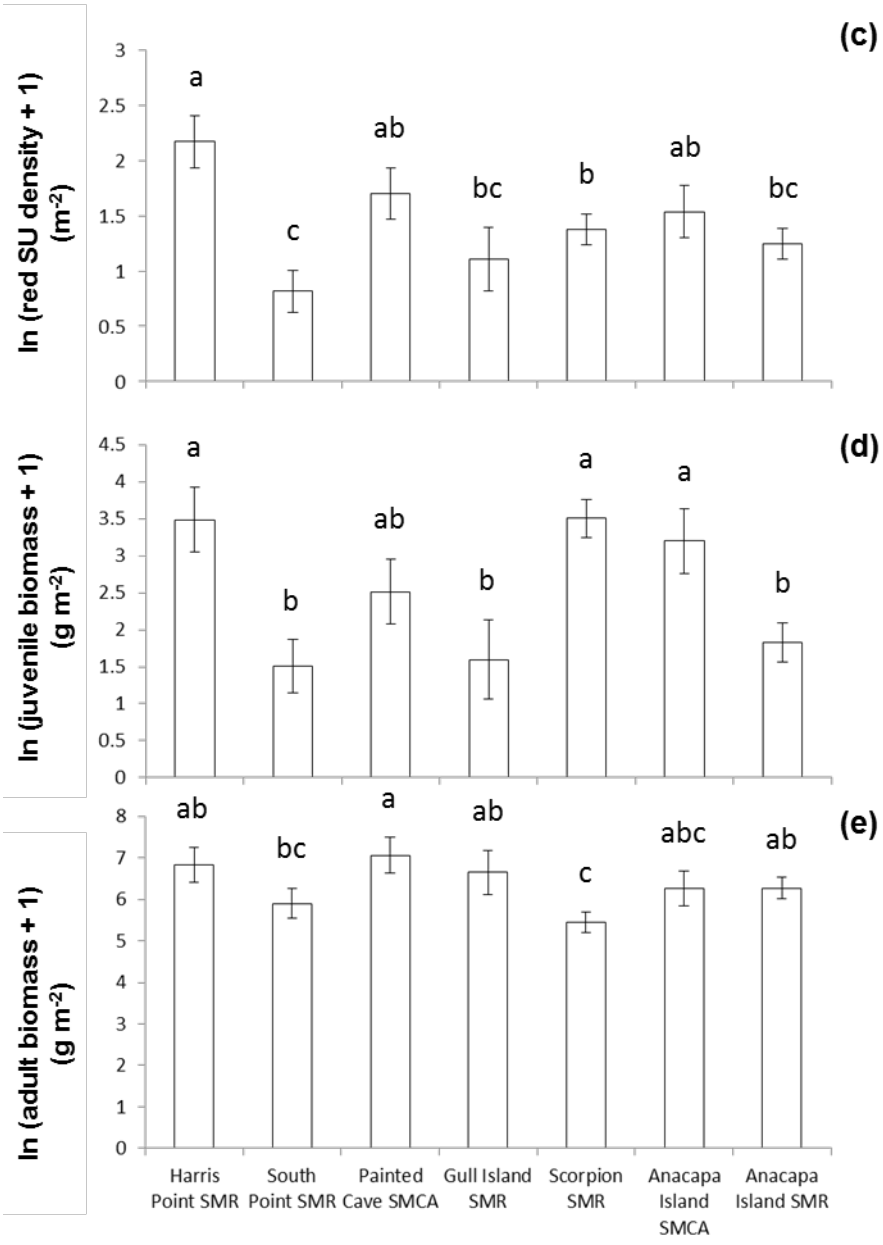
California Department of Fish and Wildlife website. Available: https://www.wildlife.ca.gov/Conservation/Marine/MPAs/Network/Southern-California (accessed 2015 August 18)

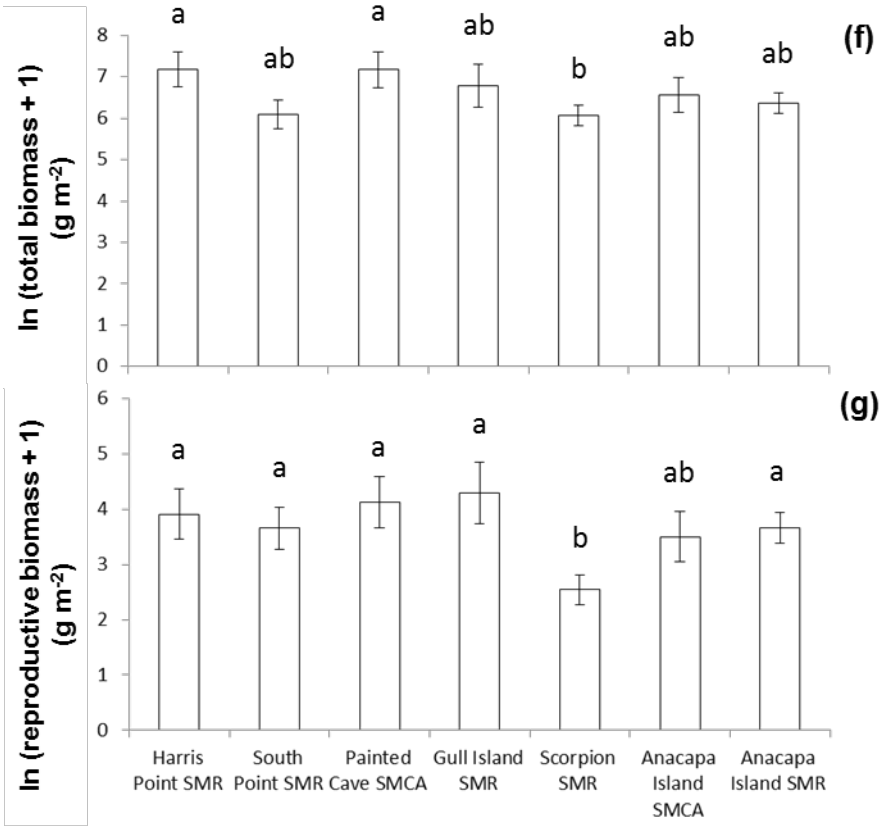
Table A1. ANOVAS across sites within the seven MPAs for mean red sea urchin (SU) gonadosomatic index (GSI), adult red SU test diameter (TD), density, juvenile biomass (25-50 mm) (juv bio), adult biomass (above 51 mm) (ad bio), total biomass (total bio), reproductive biomass (reprod), mean kelp density (kelp), and purple sea urchin density (purple).

	indiv. metrics		pop. metrics				
Response Variable	GSI	TD	density	juv bio	ad bio	total bio	reprod
R^2	0.312	0.480	0.289	0.405	0.224	0.144	0.232
F-ratio$_{6,65}$	4.46	9.08	4.00	6.69	2.83	1.65	2.97
P	0.0009	<0.0001	0.002	<0.0001	0.0172	0.1499	0.0134

Response Variable	kelp	purple
R^2	0.383	0.290
F-ratio$_{6,65}$	6.10	4.02
P	<0.0001	0.0019


(a)
mean red sea urchin gonadosomatic index
0.12
0.1
0.08
0.06
0.04
0.02
0
cd
a
cd
ab
d
bcd
bc
(b)
mean adult red sea urchin test diameter
140
120
100
80
60
40
20
0
c
a
bc
ab
d
cd
c
Harris Point SMR
South Point SMR
Painted Cave SMCA
Gull Island SMR
Scorpion SMR
Anacapa Island SMCA
Anacapa Island SMR


(c)
ln (red SU density + 1) (m-2)
3
2.5
2
1.5
1
0.5
0
a
c
ab
bc
b
ab
bc
(d)
ln (juvenile biomass + 1) (g m-2)
4.5
4
3.5
3
2.5
2
1.5
1
0.5
0
a
b
ab
b
a
a
b
(e)
ln (adult biomass + 1) (g m-2)
8
7
6
5
4
3
2
1
0
ab
bc
a
ab
c
abc
ab
Harris Point SMR
South Point SMR
Painted Cave SMCA
Gull Island SMR
Scorpion SMR
Anacapa Island SMCA
Anacapa Island SMR


ln (total biomass + 1) (g m-2)
(f)
a
ab
a
ab
b
ab
ab
ln (reproductive biomass + 1) (g m-2)
(g)
a
a
a
a
b
ab
a
Harris Point SMR
South Point SMR
Painted Cave SMCA
Gull Island SMR
Scorpion SMR
Anacapa Island SMCA
Anacapa Island SMR

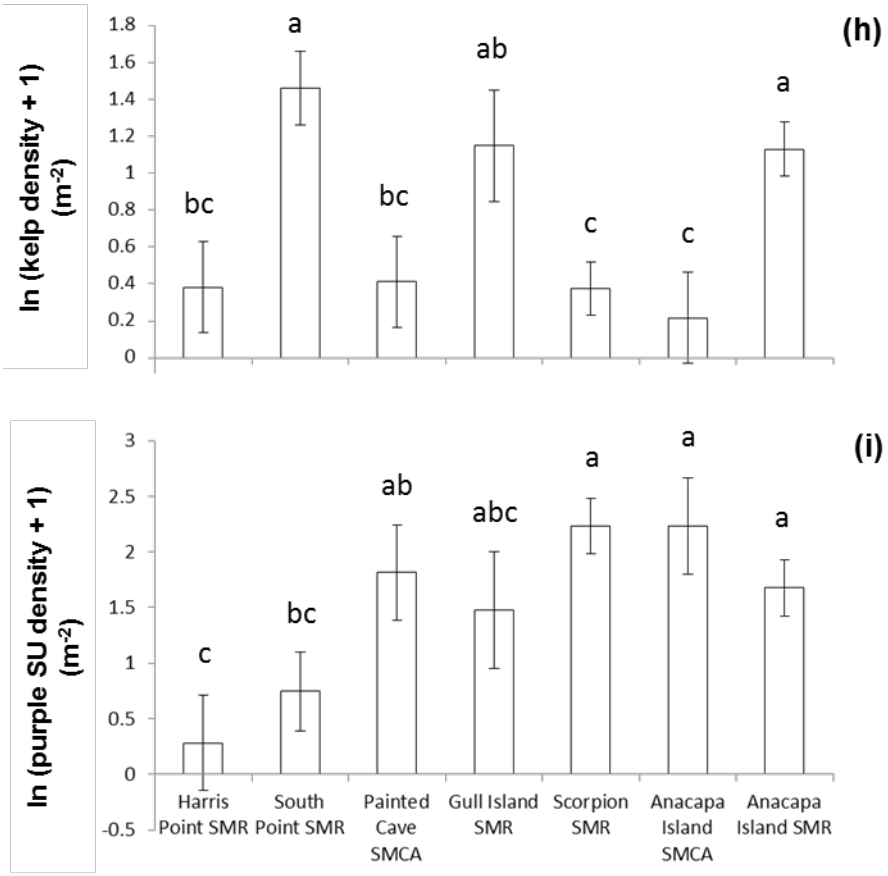


Figure A1. Mean red sea urchin (SU) (a) gonadosomatic index (GSI) and (b) adult red SU test diameter (TD), (c) density, (d) juvenile biomass (25-50 mm), (e) adult biomass (above 51 mm), (f) total biomass, (g) reproductive biomass, (h) mean kelp density, and (i) purple sea urchin density across the seven MPAs.

Appendix B
Variation in juvenile and total biomass of red sea urchins across the northern Channel Islands

We explored spatial variation in juvenile (25-50 mm) and total biomass (above 25 mm) between MPA and unprotected sites across the Channel Islands, among years, and across longitude and depth using GLM. We also explored the relative importance and interactions among our three main predictor variables (Table 1: protection from fishing (MPA versus unprotected area), mean kelp density, and mean sea surface temperature [over the previous year]) in driving variation of juvenile and total biomass.

For juvenile biomass, there were significant two-way interactions between longitude and year, longitude and protection from fishing, and longitude and depth (GLM: Table B1, Figure B1). In 2009, juvenile biomass increased from west to east; in 2010, this positive relationship was weaker; and in 2011, there was no difference across longitude. Within unprotected areas, there was a slightly positive relationship from west to east, however, within MPAs there was no difference across longitude. Finally, in shallow areas there were no differences in juvenile biomass across the region, but in deep areas there was high variability and higher juvenile biomass from west to east.

For total biomass, there was an interaction between longitude and protection from fishing; within unprotected areas there were slightly higher levels of total biomass from west to east, and the opposite relationship occurred within MPAs (slightly negative relationship between longitude and total biomass) (Table B1, Figure B1). In addition, there was a three-way interaction between longitude, year, and depth. In general there were no large differences in total biomass across longitude except for within shallow areas in 2009 and deeper areas in 2011, there were slightly higher levels of total biomass from west to east. In addition, within shallow areas in 2011, there were slightly lower levels of total biomass from west to east.

When exploring the drivers of variation in juvenile and total biomass of red sea urchins, we found significant three-way interactions among protection from fishing, temperature, and kelp density (Table B2). Within unprotected areas, kelp did not explain a significant amount of variability in juvenile biomass or total biomass of red sea urchins nor did temperature. However, within MPAs, in colder regions (in the west) there was a negative relationship with kelp density and red sea urchin juvenile biomass and a weaker negative relationship with kelp density and red sea urchin total biomass. Within MPAs in warmer regions (in the east) there was no difference in juvenile biomass across varying levels of kelp density and a slightly positive relationship with kelp density and total red sea urchin biomass.

Table B1. General linear models examining spatial variability (year, longitude, protection from fishing, and depth) across log-transformed mean red sea urchin juvenile biomass (between 25 and 50 mm) (juv bio) and total biomass (above 25 mm) (tot bio): (a) overall model R^2, F-ratio, DF, and P-values and (b) effect tests. All non-significant interaction terms were sequentially removed.

(a)

Response Variable	juv bio	tot bio
R^2	0.367	0.255
$F\text{-ratio}_{DF}$	$F_{9,142}$	$F_{13,142}$
	8.58	3.40
P	<0.0001	0.0002

(b)

		juv bio			tot bio		
Source	DF	F	*P*		F	*P*	
year	2	0.63	0.5337		0.1112	0.8949	
long	1	6.12	0.01	*	0.0121	0.9126	
year*long	2	4.17	0.0176	*	1.9172	0.1512	
MPA	1	0.10	0.757		10.498	0.0015	*
year*MPA	2						
long*MPA	1	14.53	0.0002	*	5.9072	0.0165	*
depth	1	18.70	<0.0001	*	14.7051	0.0002	*
year*depth	2				0.6626	0.5172	
long*depth	1	7.90	0.0057	*	2.969	0.0873	*
MPA*depth	1						
long*MPA*depth	1						
long*year*depth	2				3.4424	0.035	*

Table B2. General linear models examining spatial drivers (protection from fishing, kelp density, SST, and interactions) across log-transformed mean red sea urchin juvenile biomass (between 25 and 50 mm) (juv bio) and total biomass (above 25 mm) (tot bio): (a) overall model R^2, F-ratio, DF, and P-values and (b) effect tests.

(a)

	indiv. metrics	
Response Variable	juv bio	tot bio
R^2	0.332	0.161
$F\text{-ratio}_{7,142}$	9.59	3.69
P	<0.0001	0.0011

(b)

			indiv. metrics			
			juv bio		total bio	
Source	Nparm	DF	F	*P*	F	*P*
MPA	1	1	0.13	0.7195	8.43	0.0043*
kelp	1	1	21.31	<0.0001*	1.12	0.2914
MPA*kelp	1	1	6.97	0.0093*	0.27	0.6063
SST	1	1	16.12	<0.0001*	0.33	0.5691
MPA *SST	1	1	10.08	0.0019*	1.74	0.1899
kelp*SST	1	1	0.0005	0.9823	3.84	0.0521†
MPA*kelp*SST	1	1	6.16	0.0143*	6.30	0.0133*

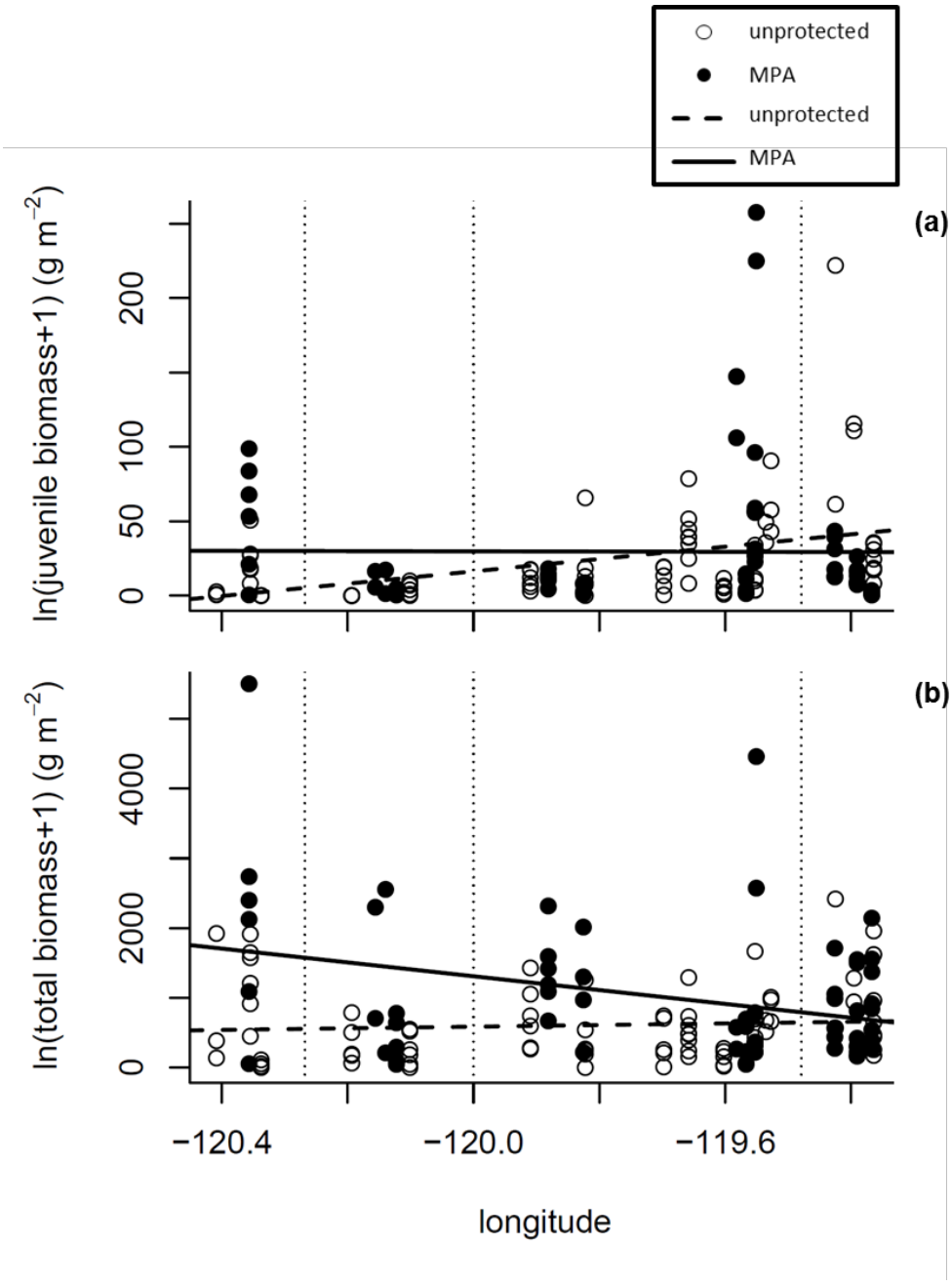


Figure B1. Mean red sea urchin (SU) (a) juvenile biomass (between 25 and 50 mm) and (b) total biomass (above 25 mm) (showing log-transformed values) across longitude from west to east (left to right) and grouped across MPA and unprotected areas. Vertical dotted lines separate the islands: San Miguel, Santa Rosa, Santa Cruz, and Anacapa Islands. Lines show linear regressions across longitude and between MPA and unprotected areas (for viewing purposes only; juvenile biomass: R^2=0.19, $F_{3,142}$=10.95, P<0.0001; total biomass: R^2=0.10, $F_{3,142}$=4.87, P=0.0030).

Appendix C
Variation in gonadosomatic index as a function of gender in red sea urchins

We did not find any consistent spatial differences in GSI across gender. Across all urchins examined, GSI was not significantly different between genders while controlling for test diameter. Nor were there differences in GSI between genders within each island.

We did identify some differences in GSI between males and females within a few sites. However, the magnitude of differences was low (see below), and the direction of the differences was not consistent. More importantly, these differences may be spurious because after FDR correction due to multiple testing, none of these p-values was significant (but see Table CI for the GSI averages per gender within those four of 30 sites with potential but non-significant differences).

When we included gender as an additional predictor within the GLM models for GSI performed in this study, it did not explain a significant amount of variation. In addition, we performed separate driver models per gender and results were very clear: kelp was the most important driver in both genders.

Table C1. The GSI averages per gender within those sites (4 of 30 sites) with potential but non-significant differences.

Site	Female GSI	Male GSI	n
Anacapa East Fish Camp	0.03	0.04	28
SCI Coche Point	0.03	0.02	29
SCI Scorpion Point	0.05	0.07	121
SCI Valley Point	0.08	0.11	77

Appendix D
Parameter estimates for GLMs and spatial driver GLMs excluding SMI

Table D1. Parameter estimates for general linear models examining (a) spatial patterns of variability (year, longitude, protection from fishing, and depth) and (b) spatial drivers of variability (protection from fishing, kelp, and SST) across red sea urchin response variables: mean red sea urchin (SU) gonadosomatic index (GSI), mean adult red SU test diameter (TD), mean red SU density (density), mean adult red SU biomass (biomass), and mean red SU reproductive biomass (reprod). For each model term, we display the parameter estimate (Est), standard error (SE), *t* Ratio, *p*-value (Prob>|t|), and the standardized beta coefficients (Beta).

(a)

	GSI					TD					density				
Term	Est	SE	t Ratio	Prob>|t|	Beta	Est	SE	t Ratio	Prob>|t|	Beta	Est	SE	t Ratio	Prob>|t|	Beta
Intercept	-3.213	1.039	-3.09	0.0024	0.000	-2056.15	426.23	-4.82	<0.0001	0.000	-7.55	18.40	-0.41	0.6821	0.000
year[2009]	-0.002	0.004	-0.40	0.6891	-0.035	5.39	1.55	3.47	0.0007	0.272	-0.01	0.06	-0.22	0.8286	-0.017
year[2010]	0.004	0.004	0.87	0.385	0.077	0.18	1.78	0.10	0.9209	0.008	-0.06	0.07	-0.77	0.4421	-0.061
longitude	-0.027	0.009	-3.16	0.0019	-0.266	-17.82	3.56	-5.00	<0.0001	-0.379	-0.08	0.15	-0.51	0.608	-0.041
MPA [unprotected]	0.000	0.003	0.17	0.8619	0.014	-3.66	1.18	-3.12	0.0022	-0.230	-0.10	0.05	-2.17	0.0319	-0.158
depth	-0.001	0.001	-0.82	0.414	-0.067	0.43	0.28	1.51	0.1335	0.111	-0.06	0.01	-5.61	<0.0001	-0.405
(longitude+119.8)*MPA[unprotected]	-0.017	0.009	-1.97	0.0507	-0.161						0.40	0.14	2.75	0.0069	0.200
(longitude+119.8)*(depth-9.6)						-2.26	0.90	-2.52	0.0128	-0.184	0.08	0.04	2.20	0.0295	0.158
year[2009]*(longitude+119.8)											0.65	0.19	3.39	0.0009	0.271
year[2010]*(longitude+119.8)											-0.29	0.21	-1.38	0.1699	-0.108

	biomass					reprod				
Term	Est	SE	t Ratio	Prob>|t|	Beta	Est	SE	t Ratio	Prob>|t|	Beta
Intercept	-44.34	44.44	-1.00	0.3201	0.000	-95.40	38.03	-2.51	0.0133	0.000
year[2009]	-0.05	0.16	-0.33	0.7423	-0.028	-0.07	0.14	-0.48	0.6288	-0.041
year[2010]	0.06	0.19	0.34	0.7354	0.029	0.07	0.16	0.46	0.6457	0.039
longitude	-0.43	0.37	-1.14	0.2543	-0.094	-0.83	0.32	-2.61	0.01	-0.212
MPA [unprotected]	-0.45	0.12	-3.63	0.0004	-0.292	-0.36	0.11	-3.43	0.0008	-0.272
depth	-0.09	0.03	-3.04	0.0028	-0.243	-0.09	0.03	-3.53	0.0006	-0.278

(b)

	GSI					TD					density				
Term	Est	SE	t Ratio	Prob>|t|	Beta	Est	SE	t Ratio	Prob>|t|	Beta	Est	SE	t Ratio	Prob>|t	Beta
Intercept	0.084	0.017	4.99	<0.0001	0.000	103.89	7.89	13.16	<0.0001	0.000	1.26	0.37	3.38	0.0009	0.000
MPA[unprotected]	0.001	0.002	0.28	0.7813	0.019	-3.52	1.11	-3.18	0.0018	-0.221	-0.11	0.05	-2.06	0.0415	-0.162
kelp	0.029	0.003	9.10	<0.0001	0.621	11.13	1.49	7.47	<0.0001	0.523	-0.31	0.07	-4.43	<0.0001	-0.353
MPA[unprotected]*(kelp)-0.80)	-0.004	0.003	-1.29	0.1993	-0.088	-5.67	1.49	-3.81	0.0002	-0.266	0.09	0.07	1.34	0.1816	0.107
SST	-0.002	0.001	-2.30	0.0229	-0.157	-1.77	0.48	-3.71	0.0003	-0.259	0.02	0.02	0.71	0.4776	0.057
MPA[unprotected]*(SST-15.6)	-0.001	0.001	-1.03	0.3049	-0.069	0.38	0.48	0.81	0.4218	0.056	0.04	0.02	1.66	0.0996	0.130
(kelp-0.80)*(SST-15.6)	0.001	0.001	0.56	0.5792	0.037	0.48	0.64	0.75	0.4548	0.051	0.07	0.03	2.14	0.0343	0.167
MPA[unprotected]*(kelp-0.80)*(SST-15.6)	0.001	0.001	1.09	0.2798	0.073	0.38	0.64	0.59	0.5546	0.041	-0.13	0.03	-4.24	<0.0001	-0.333

	biomass					reprod				
Term	Est	SE	t Ratio	Prob>|t|	Beta	Est	SE	t Ratio	Prob>|t|	Beta
Intercept	6.75	0.92	7.37	<0.0001	0.000	4.31	0.75	5.77	<0.0001	0.000
MPA[unprotected]	-0.42	0.13	-3.29	0.0013	-0.276	-0.34	0.10	-3.29	0.0013	-0.260
kelp	-0.03	0.17	-0.19	0.8458	-0.017	0.38	0.14	2.67	0.0085	0.213
MPA[unprotected]*(kelp-0.80)	-0.08	0.17	-0.49	0.6236	-0.042	-0.14	0.14	-0.99	0.3226	-0.079
SST	-0.06	0.06	-1.12	0.2668	-0.094	-0.09	0.05	-2.06	0.0417	-0.164
MPA[unprotected]*(SST-15.6)	-0.01	0.06	-0.18	0.8578	-0.015	-0.02	0.05	-0.39	0.6951	-0.031
(kelp-0.80)*(SST-15.6)	0.21	0.07	2.87	0.0047	0.239	0.20	0.06	3.31	0.0012	0.259
MPA[unprotected]*(kelp-0.80)*(SST-15.6)	-0.11	0.07	-1.49	0.1398	-0.124	-0.10	0.06	-1.71	0.0887	-0.135

Table D2. General linear model results excluding SMI examining spatial drivers of variability (protection from fishing, kelp, and SST) across red sea urchin response variables: mean red sea urchin (SU) gonadosomatic index (GSI), mean adult red SU test diameter (TD), mean red SU density (density), mean adult red SU biomass (biomass), and mean red SU reproductive biomass (reprod).

	individual metrics		population metrics		
	GSI	TD	density	biomass	reprod
Source	*P*	*P*	*P*	*P*	*P*
MPA		**		**	**
kelp	***	***	***		**
MPA*kelp		**			†
SST		**	*		
MPA *SST					
kelp*SST			†	**	***
MPA*kelp*SST	†				

† marginally significant p-value 0.05-0.10
*p≤0.05
**p≤0.01
***p≤0.001

Appendix E
Details on patterns in kelp density, purple sea urchin density

To help understand trends in the above red urchin metrics, we also examined kelp (*Macrocystis pyrifera*) density, since kelp is an important resource to sea urchins, and purple sea urchin (*Strongylocentrotus purpuratus*) density, as this species is a prime space and resource competitor to red sea urchins (Dewees 2003; Rogers-Bennett 2007). The densities of both species of sea urchins (reds and purples) were included in the model predicting kelp density, as they both likely negatively affect kelp density through grazing pressure.

Spatial patterns of kelp and purple sea urchin density

Kelp density tended to be greater in the west but only within unprotected sites (Fig. E1, Table E1). However, there was a three-way interaction among longitude, protection from fishing, and depth. Within unprotected areas kelp density decreased with depth, but within the western MPA sites kelp density increased with depth; in the east kelp density was similar across depths within our sites. Kelp density was significantly greater in 2011 than in 2009 and 2010, which were statistically similar. The strongest spatial model (R^2 0.51) was with purple sea urchin density, with significantly greater densities eastward and no differences across MPA and unprotected areas. Purple sea urchin densities also were significantly greater in shallower sites.

Note: Variation in kelp density across MPA and unprotected areas should be explored in the future, as more time since MPA establishment increases. Hamilton and Caselle (2014) did not detect differences in kelp between MPA and unprotected areas per island (in 2003-2012 data), whereas our examination (of 2009-2011 data) across longitude did reveal significant differences within the western region, where red sea urchin fishing pressure is higher.

Table E1. General linear models examining spatial variability (year, longitude, protection from fishing, and depth) across response variables: kelp density and purple sea urchin density: (a) overall model R^2, F-ratio, DF, and *P*-values and (b) effect tests. All non-significant interaction terms were sequentially removed.

(a)

	kelp	purple
R^2	0.250	0.508
F-ratio_{DF}	$F_{9,142}$	$F_{5,142}$
	4.92	28.31
P	<0.0001	<0.0001

(b)

		kelp			purple		
Source	DF	F	*P*		F	*P*	
year	2	4.16	0.0178	*	1.38	0.2544	
long	1	12.97	0.0004	*	57.15	<.0001	*
year*long	2						
MPA	1	0.34	0.5585		0.74	0.3924	
year*MPA	2						
long*MPA	1	8.82	0.0035	*			
depth	1	0.12	0.7265		54.72	<.0001	*
year*depth	2						
long*depth	1	2.39	0.1248				
MPA*depth	1	5.88	0.0166	*			
long*MPA*depth	1	4.91	0.0284	*			

*denotes significant *P*-value

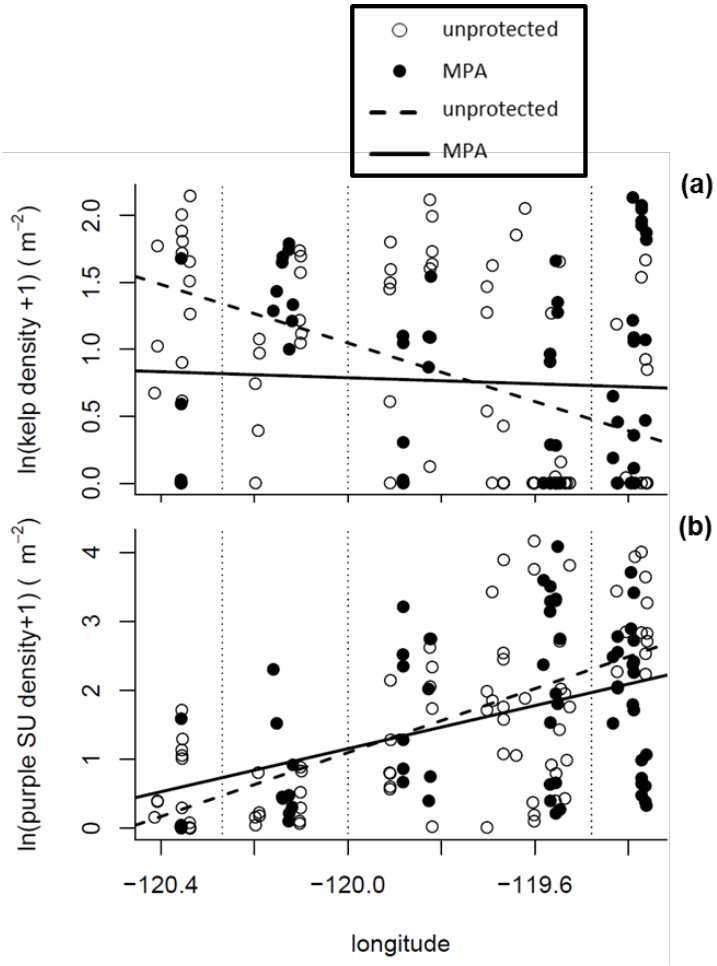


Figure E1. Mean (a) kelp density and (b) purple sea urchin density (showing log-transformed values) across longitude from west to east (left to right) and grouped by MPA and unprotected areas. Vertical dotted lines separate the islands: San Miguel, Santa Rosa, Santa Cruz, and Anacapa Islands. Lines show linear regressions across longitude and between MPA and unprotected areas (for viewing purposes only; kelp density: R^2=0.14, $F_{3,142}$=7.46, P<0.0001; purple sea urchin density: R^2=0.31, $F_{3,142}$=20.99, P<0.0001).

Appendix F
Comparing sites by MPAs-status and MPA-age

Previous work has acknowledged the difficulty in generalizing the effects of MPAs due to varying time since protection (Shears *et al.* 2012). We compared sites within the older reserve, the newer reserves, and unprotected sites to examine differences across MPA-age.

Table F1. Summary of statistical tests (t-tests and one-way ANOVAs) examining differences in our response variables (Table 1) among MPA and unprotected sites, where unprotected sites were clustered near MPAs. We examined the MPAs: South Point SMR (protected since 2003) in SRI, Scorpion SMR (protected since 2003) in SCI, and Anacapa Island SMCA (protected since 2003) and Anacapa Island SMR (protected since 1978). Within Anacapa Island, we also compared across MPA-age, comparing among sites within the unprotected area, the newer MPA, and the older MPA. The q-value is the false discovery rate (FDR) adjusted P-value due to multiple statistical tests.

	SRI			SCI			Anacapa		
	t(18)	*P*	q-value	t(26)	*P*	q-value	$F_{2,34}$	*P*	q-value
GSI	0.89	0.3863	0.4198	2.51	0.0186 *	0.0558 †	0.89	0.4198	0.4198
TD	2.32	0.0322 *	0.0966†	0.39	0.6986	0.6986	1.28	0.2911	0.43665
density	1.12	0.2769	0.4154	0.74	0.4662	0.4662	4.06	0.0269 *	0.0807 †
biomass	1.54	0.1407	0.2111	0.31	0.7555	0.7555	2.84	0.0732 †	0.21105
reprod	1.84	0.0824	0.1629	1.31	0.2014	0.2014	2.38	0.1086	0.1629
kelp	2.08	0.0525 †	0.0610†	2.04	0.0516 †	0.0610 †	4.71	0.0610 †	0.061†
purp	1.53	0.1440	0.2160	0.84	0.4061	0.4061	8.40	0.0012 *	0.0036 *

* significant P or q-values
† marginally significant P or q-values

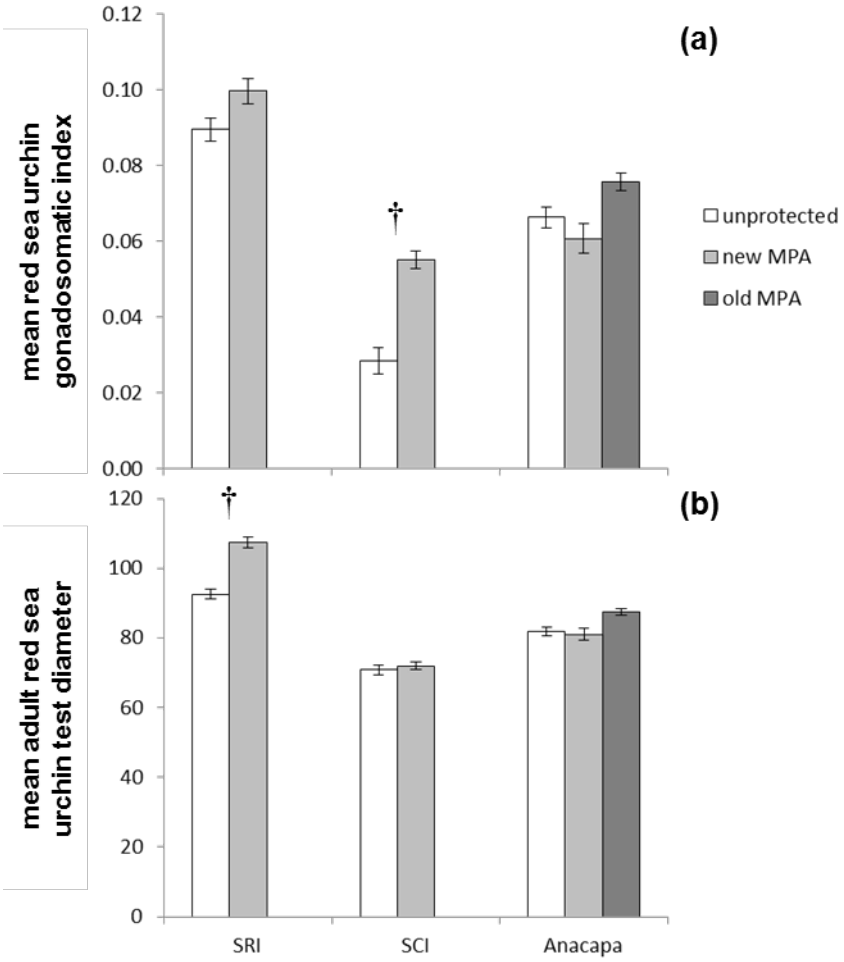
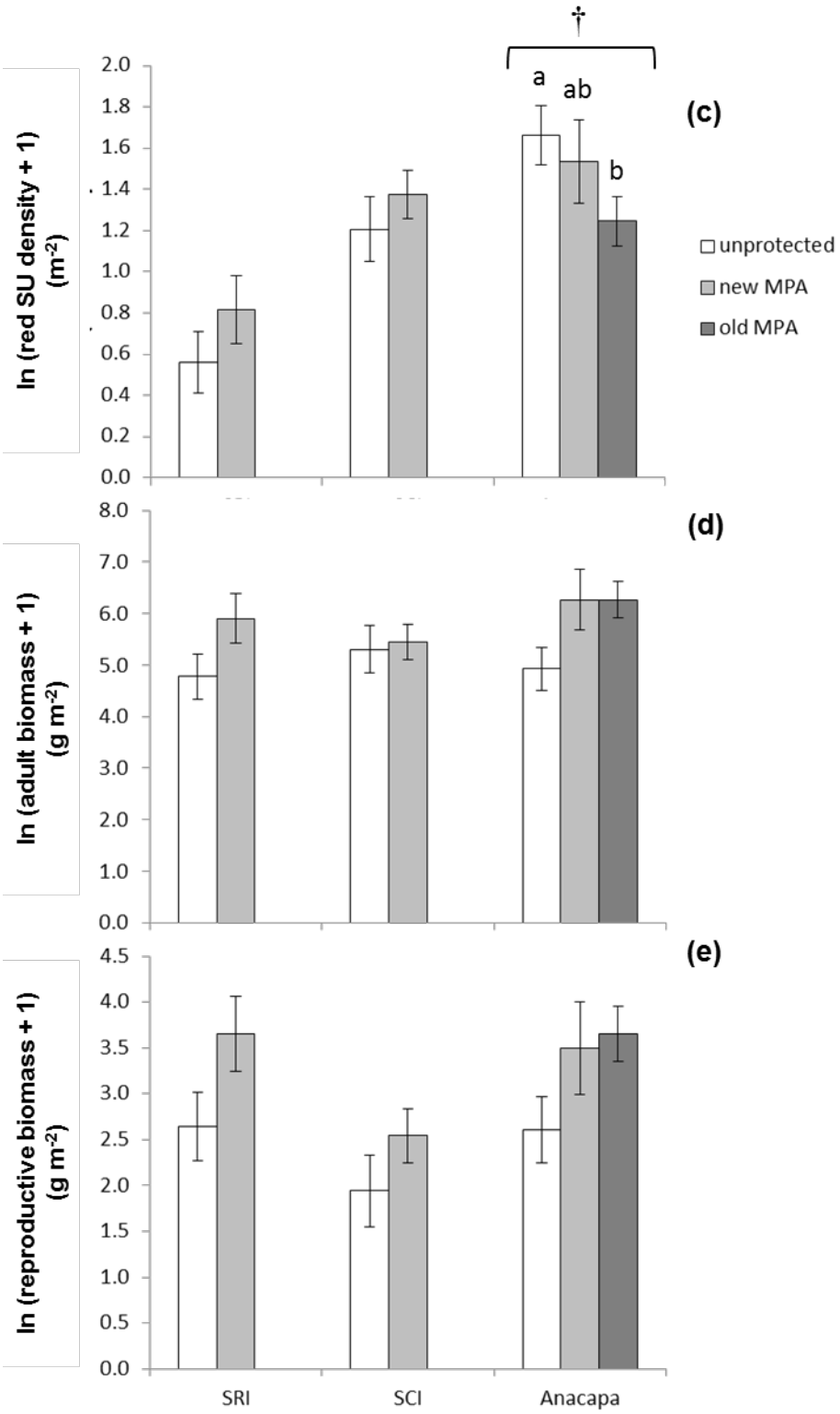


Figure F1. Mean red sea urchin (SU) (a) gonadosomatic index (GSI) and (b) adult red SU test diameter (TD), (c) density, (d) adult biomass, (e) reproductive biomass, (f) mean kelp density, and (g) purple sea urchin density (the latter five variables show log-transformed values) across MPA and unprotected areas within islands Santa Rosa Island (SRI), Santa Cruz Island (SCI) and Anacapa Island. New MPAs are South Point SMR (protected since 2003) in SRI, Scorpion SMR (protected since 2003) in SCI, and Anacapa Island SMCA (protected since 2003), the old MPA is Anacapa Island SMR (protected since 1978).
† denotes marginally significant differences
* denotes significant differences

Figure F1. continued (caption previous page).



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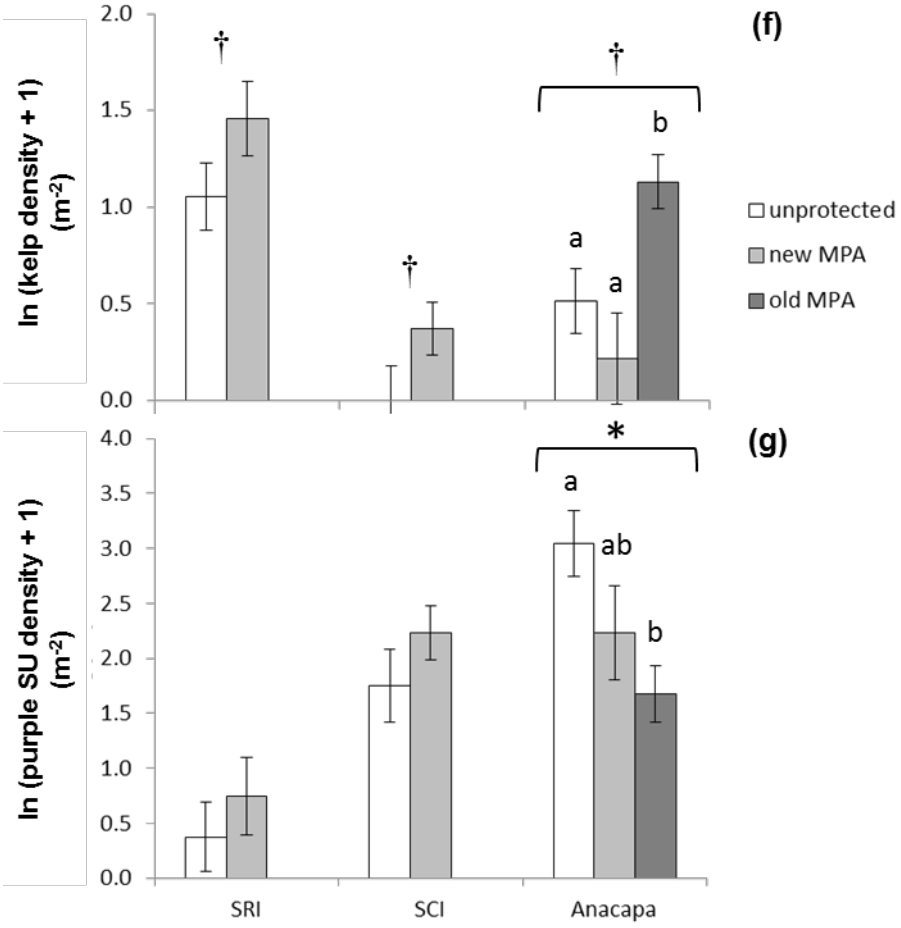

III. Quality of a fished resource: Assessing spatial and temporal dynamics

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Abstract

Understanding the spatio-temporal variability in the demography of harvested species is essential to improve sustainability if there is large geographic variation in demography. Reproductive patterns commonly vary spatially, and this is particularly important for management of "roe"-based fisheries, since profits depend on both the number and reproductive condition of individuals. The reproductive organ of the red sea urchin, *Mesocentrotus franciscanus* (previously *Strongylocentrotus* A. Agassiz, 1863), is harvested in California for the domestic and international sushi market. The primary driver of red sea urchin price within this multi-million dollar industry is gonad quality. A relatively simple measure of the fraction of the body mass that is gonad, the gonadosomatic index (GSI), provides important insight into the ecological and environmental factors associated with spatial and temporal variability in reproductive quality, and hence the value of the fishery. We used fishery-dependent samples of red sea urchins over three years to identify the seasonality of the reproductive cycle and to determine whether reproductive condition varied geographically across a heavily fished region in southern California. We also examined the responses of fishermen to the spatial and temporal dynamics of red sea

urchin reproduction using both catch and processor data. Fishermen were predictable in collecting urchins according to the seasonal reproductive dynamics of urchins, and focused their harvesting efforts in those locations where gonad quality was greatest. We demonstrate the use of red sea urchin GSI as a simple quantitative tool to predict quality, effort, landings, price, and value of the fishery. We find that current management is not effectively realizing objectives for the southern California fishery, since the reproductive cycle does not match the cycle in northern California, where management guidelines were originally shaped. Although management may not be meeting their goals, the scheme may in fact provide conservation benefits by curtailing effort during part of the high quality fishing season right before spawning.

Keywords: gonadosomatic index; Channel Islands; sea urchins; sea urchin fishery; *Mesocentrotus franciscanus*; reproduction; management

Introduction

Quality plays an important role in the price of all fish products, especially when the product is served raw. High-grade fresh fish can be worth 4 to 20 times the price of lower-grade fish (Bartram *et al.* 1996; McConnell *et al.* 1998). The manner in which a fish is caught, handled and stored affects quality and thus price (Murphy *et al.* 1995; Monfort 2002; Babcock & Weninger 2004). In addition, quality is also often related to a species' reproductive cycle. For example, in several fisheries (scallop, herring, sturgeon, squid, and salmon) quality peaks before the spawning

season (Taylor & Venn 1979; Smith 1985; Racotta *et al.* 1998; Stephenson 1999; Babcock & Weninger 2004; Iwata *et al.* 2010). Reproductive condition can vary across seasons, years, and regions due to many environmental and ecological factors, such as resource availability and quality, spawning or nursery habitat availability and quality, temperature, climate, and upwelling regime (Tegner & Dayton 1991; Montgomery & Galzin 1993; Nilo *et al.* 1997; Collins *et al.* 2000; Kreiner *et al.* 2001; Fiedler 2002; Hilborn *et al.* 2003; Babcock & Weninger 2004; Ruttenberg *et al.* 2005; Wright & Trippel 2009; Hamilton *et al.* 2011; Ebert *et al.* 2012). Understanding how reproduction in a marine resource varies can not only inform population models but also can provide insight into the value of a fished product.

When a fished species is roe-based and served raw, such as sea urchins, quality dominates product price (Unuma 2002). In recent decades, hundreds of millions of pounds of red sea urchins have been hand collected by commercial fishermen diving in California's coastal waters (California Department of Fish and Wildlife [CDFW] data www.wildlife.ca.gov/Conservation/Marine/Invertebrates/Sea-Urchin). This multi-million dollar industry relies on a consistent, fresh product, and is marketed as the sushi product *uni*. The principal sea urchin species exploited in California is the red sea urchin, *Mesocentrotus franciscanus* (previously *Strongylocentrotus* A. Agassiz, 1863). Currently California supplies about 80% of the domestic market for uni, but more than 50% of the annual harvest (by volume) is exported (D. Rudie, pers. comm.; see Appendix A for more details). Once sea urchin divers bring their

catch to shore, the gonads are typically processed, packaged into bamboo boxes, and shipped overnight to buyers.

Knowledge about spatial and temporal variability in sea urchin reproduction has been used previously to inform management, resulting in seasonal closures that serve to limit harvest during a particular reproductive season. The seasonal management scheme in California was modeled after the state of Washington's fishery, where harvest is closed during the season with low gonad quality. The rationale was that it would be economically advantageous to limit effort during the period of lowest gonad yield (P. Kalvass pers. comm.). The California Department of Fish and Wildlife (CDFW) partially based California's state-wide seasonal regulations on data from a two-year period (1991-1992) of red sea urchin processor gonad and price data from northern California (Kalvass & Hendrix 1997). Managers in California advocated a complete summer closure, when gonad quality, size, and thus prices were low due to spawning activity during the spring and summer (Ebert *et al.* 1994). However, managers compromised with the industry and instead established partial seasonal closures (P. Kalvass pers. comm.). Currently the fishery is limited to four days per week from June through October across the entire state of California and is open the rest of the year. The key question is whether a single seasonal regulation makes sense for a state with such diverse ecological regions, spanning two marine provinces (Spalding *et al.* 2007). Because the majority of the state's red sea urchin landings originate from Southern California, regulations based on the reproductive dynamics in Northern California may be inappropriate. In this study, we investigated

the fishery within the northern Channel Islands where the majority of the state's fishing occurs (CDFW data). Our research focused on three objectives: (1) to evaluate the spatial and seasonal dynamics of the red sea urchin reproductive cycle and its impact on the industry's revenues; (2) to assess fishing patterns across the regulatory time periods, seasons, and region; and (3) to quantify how fishermen respond to urchin reproductive dynamics, relating fishing effort, landings, price, and value to spatial and temporal variation in red sea urchin reproductive condition.

Our first objective focused on the evaluation of the annual reproductive cycle for sea urchins and how it varied across the northern Channel Islands. In the ecological literature, reproductive condition (i.e., a proxy of potential reproductive output) is often measured as gonadosomatic index (GSI); i.e., the ratio of wet gonad weight to wet whole weight (Ebert *et al.* 2011). This metric is simple and objective. It can be easily measured in the laboratory or on a boat or dock. It is also quantitative, rather than the qualitative processor grading scale that is typically employed by buyers in the industry. Gonadosomatic index is predictable across the various stages in the reproductive cycle (Kreiner *et al.* 2001; Ebert *et al.* 2011), so it is a simple way to compare demographics among seasons and areas.

The price differential paid for sea urchin roe across varying reproductive stages can be substantial (Kalvass & Hendrix 1997; Unuma 2002), which creates a strong incentive for selectively harvesting in the best locations and at the best times during the year. Before the sea urchin spawns, its gonad is firm. The gonad reaches its maximum size (highest GSI) just before spawning begins and subsequently shrinks

as more gametes are released (Lasker & Giese 1954; Unuma 2002; Ebert *et al.* 2012; Arafa *et al.* 2012). Once a sea urchin has spawned (lowest GSI), the gonad is characterized by a grainy and watery texture, resulting in poorer quality for consumers. In this study, we investigate whether GSI can also be an effective indicator of gonad quality, and thus the quality component of price. Although price may reflect the seasonal demand and supply, the grade of a sea urchin has a large influence on its price. When grading the quality of sea urchin for sushi, processors consider size and several qualitative measures, such as taste, shape, color, texture, and firmness (Unuma 2002; see Appendix A for more details on sushi grades). If GSI is a good proxy for the industry's quality metric, it can be used as a quantitative measure to predict the potential seasonal value of sea urchins.

To examine our second objective, we investigated how management restrictions influence fishing behavior. To this end, we compared effort and landings during the period of limited fishing (four days per week during June-October) and the period with unlimited fishing (November-May). We also assessed seasonal differences in red sea urchin price and total value. Historical effort data showed that the western region was more heavily fished than the eastern region (Shears *et al.* 2012), and we suspected this was largely due to geographic differences in roe quality and value.

Finally, our third objective was to investigate how fishermen respond to variation in reproductive condition of red sea urchins. We explored patterns in fishing behavior, including whether fishermen on average harvest more in peak quality seasons and locations to garner better prices. We tested whether the industry's effort,

total landings, and value were correlated with the seasonal patterns in the demographic measure of GSI. If global prices vary widely, local quality in the product may play a minor role in determining prices. Conversely, if variation in urchin prices is driven mostly by urchin quality, as measured by GSI, rather than global fluctuations in supply and demand, seasonal and geographical patterns of GSI could give insight into both sea urchin demographics and the resulting behavior of fishermen.

Methods

Red sea urchin seasonal reproductive cycle

To examine spatial and seasonal variability in red sea urchin reproductive condition, we sampled catch from commercial fishermen at the port of Santa Barbara approximately once per month from December 2008 to December 2011. We purchased between 10 and 30 haphazardly selected red sea urchins per haphazardly selected boat per sampling date (total n=2759 urchins). On average we sampled from nine boats per month (n=40 unique boats total; on average 24 boats per year). All sea urchins were harvested from San Miguel Island (SMI), Santa Rosa Island (SRI), and Santa Cruz Island (SCI) (Fig. 1).

Gonadosomatic index (GSI) reflects the degree of gonadal development and is defined as the ratio of gonad weight to the total sea urchin weight:

$$\text{GSI} = \text{gonad wet weight} / \text{total wet weight}. \quad (1)$$

We calculated mean GSI per boat sampled per month as an independent replicate (n=258 sampling events).

To explore whether reproductive seasonality differed across gender and regions, we performed a three-way ANOVA with gender, island, and month predicting GSI for the ten months where we had samples across all three islands. Since two months did not include port-sampled red sea urchins from all three islands, a single model testing differences across all months and islands was not possible. Therefore, we assessed differences in GSI among islands for the two months with missing data (January and November) as a separate analysis and corrected for multiple tests using false discovery rate (FDR) adjusted p-values. For both ANOVAs, we sequentially removed non-significant interaction terms (above P>0.05).

Finally, we fitted a polynomial regression to each island in order to describe the functional forms of seasonal variation in GSI across islands.

Red sea urchin industry quality

We requested data from seven processor companies who buy urchins from the Port of Santa Barbara. Only one processor was willing to provide data. We asked 18 divers for permission to use their fishing data from the single processor. Ten divers agreed to the use of their data, and these divers were responsible for providing 53% of our port samples. To compare GSI with the industry's measure of sea urchin quality, we obtained data from the processor that included: date landed, price (USD) paid to the diver per load, weight of the highest quality sea urchin gonads (grade A

and grade B uni; see Appendix A for more details on processor grading system and patterns), and weight of total load (whole sea urchins weighed at the dock). Using these data, we calculated the *processor quality index* (PQI) per fishing trip:

PQI = (grade A total gonad weight + grade B total gonad weight) / total load weight. (2)

The PQI is commonly referred to as *yield* or *gonad yield* within the sea urchin fishing industry and indicates the fraction of high valuable product extracted from the entire catch.

Since price can fluctuate based on supply and demand of both domestic and international markets, we evaluated if local quality predicts price of red sea urchins despite temporal fluctuations in prices driven by global variation in supply and demand. We used linear regression to predict mean price per kilogram from the monthly mean PQI. In addition, we tested whether the seasonal variability in red sea urchins' gonads relate to processor's perceptions of gonad quality. We tested how well the red sea urchin's reproductive cycle (monthly mean port-sampling GSI) predicts the quality of sea urchin uni (monthly mean PQI) using linear regression.

Comparing fishing metrics between regulatory time periods

To examine potential differences in fishing behavior across regulatory time periods, we examined total effort and total landings (kg). The CDFW requires commercial sea urchin fishermen to submit a landing receipt for each trip containing information including fishing location and weight of the entire catch landed at the

dock before sea urchins are processed. Total effort was measured as the sum of landing receipts submitted to CDFW per month. Since there are no comprehensive data on hours spent diving per trip, CDFW often uses the number of receipts as a proxy for effort. Since divers occasionally report multi-day trips on one landing receipt, this estimate of effort is likely an underestimate of total days of fishing. Total landings were the sum of landings (in kilograms) reported to CDFW per month.

In order to compare fishing effort during the limited versus the unlimited fishing time periods, we examined statistical differences (using ANOVA) in CDFW monthly total effort and total landings during 2009-2011 within the Channel Islands. We also included CDFW data from the port of Fort Bragg to assess whether there were fishing behavior differences across management time periods within the region where the limited-fishing season was initially based.

Regional and seasonal fishing patterns

To examine regional and seasonal fishing patterns, we examined four fishing metrics (total effort, total landings, mean price, and total value) per month during 2009-2011 in the Channel Islands (Fig. 1). Effort and landings are explained in the section above. Mean price was the average price (per kilogram) of landed red sea urchins reported to CDFW per month. Total value was calculated as the monthly sum ($US) paid to all sea urchin fishermen as recorded by CDFW.

The Channel Islands region was divided into 4 subregions based on location, as recorded in the CDFW landing receipts, using 10 x 10 minute numbered blocks: *west*

included all of SMI and the western tip of SRI, *central* included the majority of SRI and the western tip of SCI, *east* included the majority of SCI, and *Anacapa* included the entire island of Anacapa. All subregions included four CDFW blocks, except Anacapa, which only included two blocks.

To evaluate regional variability in the red sea urchin commercial fishing data, we performed a series of ANOVAs, using the four monthly fisheries metrics across subregions. We corrected for multiple tests using false discovery rate (FDR) adjusted p-values.

Finally, to evaluate fishing effort and landings across regions during the times of peak and trough of the red sea urchin reproductive cycle, we performed ANOVAs across the subregions during the months when GSI is lowest (April through June) and highest (September through December). We included region, season, and the region by season interaction to predict effort and landings.

Relating commercial fishing data to red sea urchin reproduction

We tested whether the seasonal reproductive stage, measured as GSI, was a good predictor of fishing behavior (effort and landings), red sea urchin price, and value using CDFW metrics. We used the fisheries data across the same years of our GSI samples (2009-2011) and across all available data from previous years of the fishery (1978-2008) with the rationale that seasonal fishing behavior was likely to be driven by knowledge of red sea urchin reproductive dynamics and the assumption that the red sea urchin's reproductive cycle has remained relatively consistent over the years.

We have evidence from a limited 7-month study performed in the Channel Islands that GSI had a similar cycle (Kato & Schroeter 1985).

Since the majority (72%) of our port sampling came from the western four blocks within the northern Channel Islands, we had more consistent monthly data from this area. We compared the average monthly GSI from these western samples to the monthly total effort, total landings, mean price, and total value data from these same locations using linear regression.

Results

Red sea urchin seasonal reproductive cycle

Red sea urchin GSI was highest in the fall (November GSI = 0.157 ± 0.0045) and lowest in the spring (April GSI = 0.080 ± 0.002; May GSI = 0.085 ± 0.003) (Table 1, Fig. 2; see Appendix B for a detailed summary of port-sampled red sea urchins). Based on the three years of our sampling, red sea urchins tend to take longer to build up their gonads from the late spring to the fall (around May-November) than to spawn (around December-April) (see Appendix B, Table B4 for details on evidence of spawning during our dissections).

Gonadosomatic index varied among regions in a marked, but complex, seasonal pattern (ANOVA: $F_{30,2496}=34.7$, $P<0.0001$, $R^2=0.30$; Appendix B). When we examined the 10 months of GSI means across the three islands, GSI differences among the islands were greatest during the two extreme periods of the reproductive cycle – the peak of GSI (September through December) and the trough of GSI (April

and May) (Fig. 2, Appendix B). The GSI gradient among islands flipped directions during these periods. At its peak, GSI decreased from west to east (by about 13% in December), while at the trough of the reproductive cycle, GSI increased from east to west (by about 32% in April). The GSI of sea urchins from the most easterly island (SCI) was the least variable across seasons. Within the two months (January and November) when we had samples only from SMI and SRI, there were no differences between the two islands, but GSI in November was significantly higher than in January (ANOVA: $F_{3,210}$=22.3, *P*<0.0001, R^2=0.24; Appendix B). Gender was not a significant predictor in either model (nor were there significant interactions with month or island) and was not considered further.

The quartic polynomial regressions characterized the seasonal changes in red sea urchin GSI and how GSI varied from island to island (Fig. 2; all *P*-values <0.0001).

Red sea urchin industry quality

The reproductive cycle of red sea urchins, processor gonad quality, and price were tightly correlated. Monthly mean red sea urchin GSI was a significant positive predictor of our processor quality index (PQI) (linear regression: R^2=0.87; Fig. 3a). In addition, PQI was a strong positive predictor of mean processor price per kg (US$) (linear regression: R^2=0.90; Fig. 3b). Price is largely determined by quality rather than fluctuations in global market drivers.

Comparing fishing metrics between regulatory time periods

Monthly total effort and total landings did not differ significantly between the limited versus the unlimited fishing management season (limited: June-October and unlimited: November-May) within either the Channel Islands or Fort Bragg regions (Table 2; Fig. 4). In the model examining differences in total effort, there was a marginally significant interaction term with region and management season. Within Fort Bragg there were clearly no differences in either metric between seasons, but within the Channel Islands there was a trend of greater total effort (number of receipts) during those months limited to a four-day work-week compared to the unlimited period. Both fishing metrics were higher within the Channel Islands than in Fort Bragg.

Regional and seasonal fishing patterns

Although there were no significant differences among metrics between the two regulatory time periods, we found significant regional and seasonal variability in fishery metrics (monthly total effort, total landings, mean price, and total value) during 2009-2011 (Fig. 4, Table 3). Among the three subregions, the most heavily fished west subregion, showed the greatest seasonal variation in monthly total effort, total landings, and total value (based on the higher CVs, Table 3a). Levels of these three fishery metrics generally were lower in the spring and higher in the fall and winter (Fig. 4). Mean prices of red sea urchins from the two western subregions showed a similar magnitude of intra-annual variability (the CVs were comparable, Table 3a). In addition, within all three subregions, mean prices generally increased

from February through the end of the year (Fig. 4c). Since total effort, landings, and value from Anacapa were very low, we excluded this subregion from further analyses. Within the Channel Islands region, all fishery metrics (other than price) decreased from west to east (ANOVAs, Table 3b). Total effort, landings, and value in the west were on average about 48% higher than in the central subregion and 70% higher than in the east subregion (Table 3b). On average prices within the west and central subregions were 11% higher than in the east subregion (Table 3b). False discovery rate (FDR) indicated that the p-values for these four tests did not need to be adjusted.

Finally, when we evaluated regional fishing effort and landings during the times of the peak red sea urchin reproductive cycle (the months of September through December), we found significant differences across the three subregions (Table 4). Regional patterns in effort and landings during the months of peak GSI were similar to the average annual differences, with the west on average 52% higher than the central subregion, and 73% higher than the east subregion (Table 4). However, during the months when GSI is lowest (April through June), the three subregions were more similar in effort, landings, and price. Despite this, the west subregion had effort and landings that were higher than the other subregions, but the central and east subregions were not significantly different and were on average only 44% lower than the west subregion.

Relating commercial fishing data to red sea urchin reproduction

Not surprisingly, within the most heavily fished subregion (the west) on a monthly basis, sea urchin fishermen predictably harvest red sea urchins according to their reproductive cycle. As red sea urchin gonadosomatic index (GSI) increased, monthly total effort, total landings, mean price, and total value significantly increased during 2009-2011 (linear regressions: all *P*-values<0.007; Fig. 5). These patterns were mirrored in the historical time period (1978-2008). When red sea urchin gonad condition was greatest, fisherman on average expended greater effort and produced larger landings, which is consistent with the higher prices paid to fishermen during the peak season. Conversely, when gonad quality was poorer, fishermen tended to fish less for urchins, and they received lower prices.

Discussion

We observed spatial and temporal differences in red sea urchin reproduction, which explained much of the seasonal and spatial variation in fishing effort, landings, and urchin value. Red sea urchins exhibited a pronounced annual reproductive cycle in the northern Channel Islands that differed substantially from patterns in northern California. As a result, the efficacy of a fishing regulations developed based on seasonal dynamics in northern California may be compromised. A better understanding of the linkages between sea urchin reproduction and fishing behavior could help managers make more effective decisions.

No previous studies have described in detail the entire annual reproductive cycle of the red sea urchins in the heavily fished region of the Channel Islands. Our results

show the spawning period in the northern Channel Islands occurred over roughly five months (December-April), and the building, or gonad growth, period occurred over roughly seven months (May-November) (Fig. 2). The seasonal patterns we found in the reproductive cycle (GSI) and processor gonad-yields (PQI) generally match those reported in a limited 7-month study that took place in the early years of the fishery (1970's) on San Miguel and Santa Cruz Islands (Kato and Schroeder, 1985). In addition, Ebert and colleagues (1994) reviewed literature reporting a similar winter to spring timing of spawning for red sea urchins in southern California. Furthermore, spawning in northern California was noted to be later, occurring in the spring to summer seasons (Ebert *et al.* 1994). In addition, previous research on the co-occurring purple sea urchin *Strongylocentrotus purpuratus* reports a similar annual cycle (Gonor 1972; Pearse, Pearse & Davis 1986; Lester *et al.* 2007).

Typically, urchins spawn just after they reach their peak in gonad size. When they are done spawning, they reach their minimum size. Urchins increase in gonad size due to the growth of nutritive phagocytes (NPs) (Unuma 2002; Walker *et al.* 2007), for red sea urchins this occurs during the summer as they consume abundant drift kelp. Then these NPs support the growth and development of the germ cells (GCs) just before and during the spawning season (Unuma 2002; Walker *et al.* 2005, 2007). Spawning generally indicates lower quality. Uni (urchin sushi) buyers do not like the texture of spawning gonads (Bernard 1977; Unuma 2002). During, the first month of the spawning season (December) prices are still relatively high but then they drop rapidly as spawning continues January through April. The reproductive

"ripeness," or fully mature gonads at the end of gametogenesis, occurs during the spawning season when most of the nutritive phagocytes have shrunken (Unuma 2002). This is the season when sushi quality declines as GSI declines.

As in many species, these seasonal patterns of reproduction may be driven by seasonal patterns in resource abundance or quality for adults or larval stages (Lasker & Giese 1954; Bennett & Giese 1955; Ebert 1968; Bernard 1977; Bronstein & Loya 2015). Previous studies have shown that food availability and quality for adult sea urchins influences gonad quality (Keats *et al.* 1984; Vadas Sr. *et al.* 2000; Claisse *et al.* 2013). In the spring months, kelp begins to recover from winter storm disturbance (Cavanaugh *et al.* 2011), which is synchronous with the increase in red sea urchin allocation to reproductive growth. There is high inter-annual variability in kelp canopy biomass, but it generally peaks at SMI, SRI and SCI around June through August (Cavanaugh *et al.* 2011; Bell *et al.* 2015b) during the period of peak GSI increase. In addition, drift kelp, an important resource for sea urchins, tends to be higher in the summer and fall, when kelp biomass is higher and water movement is lower (Harrold & Reed 1985). Following the timing of high abundance of drift kelp, purple sea urchins have shown subsequent peaks in gonad indices (Basch & Tegner 2007). Within our study region, kelp canopy biomass is generally lowest in the winter months due to age-dependent mortality (Rodriguez *et al.* 2013) and disturbance in response to increased wave heights from winter storms (Reed *et al.* Arkema 2008; Cavanaugh *et al.* 2011; Bell *et al.* 2015a). The spawning period of red sea urchins coincides with the period of minimum kelp biomass. Thus, spawning

occurs in the months when resources for adults are more limited, so there is less opportunity to garner new resources to support gonadal growth.

As with other urchin species, if food is limiting to larval success, we would expect spawning to coincide also with phytoplankton blooms (the primary resource for the larval stages of sea urchin), rather than temperature (Himmelman 1978; Starr *et al.* 1990; Bronstein & Loya 2015). Recent data (1997-2010) suggest that the Santa Barbara Channel experiences extreme inter-annual variability in the timing of chlorophyll peaks, but in general blooms begin between March and June, with some years starting in February and some peaking in September (Otero & Siegel 2004; F. Henderikx Freitas, pers. comm). However, red sea urchin spawning begins and peaks in December and January and appears to continue through June (Appendix B). While the timing of peaks in phytoplankton and red sea urchin spawning do not appear to be perfectly aligned, the month of lowest levels of chlorophyll and highest sea surface temperatures in September coincides with the lowest spawning levels (Appendix B; Otero & Siegel 2004). Sea urchin larvae begin to feed within the first week of life and remain in the water column for about 40 days (ranging from 27 to 131 days depending on food and temperature; Hinegardner 1969; Rogers-Bennett 2007). The reproductive timing of red sea urchins is likely tightly linked with both adult resources (kelp) and larval resources (phytoplankton) (Giese 1959). However, further studies are needed to disentangle the relative influence of temperature and food availability (specific to various life-cycle stages) on the reproductive timing of sea urchins.

Fishermen respond to red sea urchin reproductive variability due to differences in roe quality and price. Our results indicate that red sea urchins are more valuable in the western channel, especially during peak GSI in the fall. Consistent with this pattern, fishermen harvest more in western locations than eastern locations, especially during this period (Fig. 4; Table 4; Shears *et al.* 2012). By contrast, during the trough of the reproductive season, GSI showed the opposite spatial pattern – lower in the west than in the east (Table 1, Appendix B). Fishermen changed their regional fishing behavior during the trough of the reproductive season; fishermen still fished more in the west subregion, but the regional differences in fishing effort and landings were not nearly as pronounced during this time of year (Table 4). There were no significant differences in effort and landings between the central and east subregions (Table 4). Fishermen likely do not more aggressively switch to harvesting in east during the period of low GSI because of the higher abundance of larger and potentially more valuable urchins in the western regions (Teck *et al*, in prep).

When we examined the most heavily fished subregion, the west, we found that high temporal variation in the quality of a fished resource drove predictable seasonal patterns of fishing. We found that quality, total effort, total landings, mean price, and total value in sea urchins harvested from the Channel Islands are highly predictable based on the reproductive cycle, measured here as GSI. These relationships between the fishery metrics and GSI during our sampling period (2009-2011) were highly significant. In addition, we used these GSI data to predict historical metrics of the fishery (1978-2008). These relationships were similar and stronger indicating that the

red sea urchin's reproductive cycle has been a strong driver of the sea urchin industry patterns over those 30 years of the fishery. Our results from southern California agreed with historical data from northern California showing gonad yield and price to be positively correlated (Figs. 3 and 5; Kalvass & Hendrix, 1997). However, historically the catch in northern California was inversely related to price (data 1985-1994; Kalvass & Hendrix, 1997), which was contrary to our findings. Fishermen may have been somewhat limited by unsafe boating conditions in the winter, when prices tended to be higher in northern California (Kalvass & Hendrix 1997), and because of these constraints they fished more during the season of low prices.

Management restrictions were established in California in order to limit harvest during the low gonad quality season with the rationale that if effort needs to be limited to regulate overall catch, the costs would be smaller if sea urchin fishermen had greater effort during a season of higher quality. This statewide management scheme was based on the cycle of the northern California red sea urchin; managers attempted to limit effort during the season with low quality and prices (in the late spring to fall months) (Fig. 6). Currently, fewer work-days are allowed during the months of June through October, but in southern California this is the middle through nearly the end of the gonadal growth period (Fig. 2 and 6). These months of restricted fishing include several months when fishermen received some of the highest prices (see Appendix C, Table C1).

We found that despite these attempted effort restrictions, fishermen followed the sea urchin reproductive cycle and countered the effort restrictions. The time of the

year with a limited number of allowable fishing days did not result in significantly lower monthly effort (number of days fished) than the rest of the year (Table 2). If anything, there was a weak trend that effort and prices were lower within the Channel Islands during the unlimited season, which reflects the fact that this unlimited time-period contained the months with the lowest GSI (Fig. 2). Part of the unlimited time-period also coincides with more frequent storms and high wind speeds of winter and spring (Harms & Winant 1998; Byrnes *et al.* 2011), which may also limit fishing trips statewide. Our results show that the period of low prices, low quality, and spawning at the Channel Islands (winter to spring) generally did not coincide with the period during which managers attempt to curtail effort through limiting allowable days fishing (summer to fall) (Fig. 6). These findings clearly show that manager's interest in curtailing effort when it was purportedly least costly is ineffective in reducing effort to levels below the unmanaged season. As with other open access fisheries, there is little incentive to conserve or limit harvest (Berkes *et al.* 2006), especially during a highly-profitable season. Sea urchin processors and buyers have specifically recommended adding one more open day per week to the summer to early fall months when demand is also high in the US market (California Sea Urchin Commission (CSUC) 2014) to enhance the profitability of the fishery. However, it is unknown whether the resource could sustain up to 14% more intense fishing (by adding one day) during this season, which occurs right before sea urchins spawn. The current restrictions in southern California, may in fact be providing a conservation benefit to the fishery.

Our results, while underscoring the tight link between variability in a resource and fishing, are not embedded in a static world. We have quantified the extent to which reproductive cycles can drive seasonal quality in a resource, which in turn can influence price and thus fishing effort. Future key research should include a consideration of how climate may influence both resource dynamics and fishing behavior. Changes in climate (e.g., increases in temperature, storm severity, and storm frequency) may result in both profound ecological ramifications (Mos *et al.* In press; Hughes 2000; Harley *et al.* 2006) and varying fishing behavior (Chollett *et al.* 2014). For example, if storms increase during the winter, fishing effort during the high quality gonad season may be more limited. If the higher frequency of storms and increased wave action reduces kelp density, gonad quality may be degraded in certain areas that were once important fishing grounds. In addition, since climate and fishing both influence species' distribution and abundance, it is important to understand their combined effects on the system may be synergistic (Harley & Rogers-Bennett 2004). Examining phenological changes in species, which may include tracking reproduction over seasons and years, is not only important for resource management but also may be a simple ecological indicator of climate change (Edwards & Richardson 2004).

Acknowledgements

Special thanks to the many commercial sea urchin fishermen out of the Port of Santa Barbara who participated in this study; to Stephanie Mutz, who initiated sampling efforts at the port of Santa Barbara, and for helpful conversations about the fishery; to the weigh-masters, especially Wes Carpenter, without whom this research would not have been possible; to the Santa Barbara Fish Market, especially Brian

Colgate; to Claudia Scianna and the numerous undergraduate and high school students who assisted in collections and in laboratory processing (including M. Adams, A. Alger, G. Alongi, K. Asanion, M. Bogeberg, E. Casas, J. Conley, D. Cooper, C. Fitzgerald, S. Ginther, M. Hunt, W. Meinhold, S. Meinhold, A. Poppenwimer, A. Quintana, T. Rogier, J. Roh, R. Shen, T. Shultz, A. Stroud, K. Treiberg, O. Turnross, and A. Wong); to Pete Kalvass, California Department of Fish and Wildlife, for providing commercial sea urchin data and engaging in insightful conversations about the fishery; and to Dave Rudie, Catalina Offshore Products, for providing valuable price and quality data, and information from the industry side of the fishery. We are further grateful to the ten anonymous fishermen who granted permission to use processor data on the sea urchins they collected. We thank Jim Carlton, Jenn Caselle, Jorge Cornejo, Scott Hamilton, Jeremy Prince, Bob Warner, and Jono Wilson for comments on an earlier version of this manuscript. This work was supported in part by the Henry Luce Foundation's Luce Environmental Science to Solutions Fellowship and the Nejat B. Ezal Memorial Fellowship Award. Our work was approved by the Human Subjects Committee in the Office of Research at UCSB.

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Tables

Table 1. Summary of port sampling of red sea urchins: mean gonadosomatic index (GSI) per month, sample size of boats (N_b) and individual red sea urchins (N_u), and one standard error (SE), which was calculated using N_u. Total shows average GSI across all months and the sum of each sample size type. (See Appendix B for month by island differences.)

	SMI				SRI				SCI†				overall	
month	GSI	Nb	Nu	SE	GSI	Nb	Nu	SE	GSI	Nb	Nu	SE	GSI	SE
1	0.1068	3	40	0.0049	0.1120	5	55	0.0046	.		0	.	0.110	0.003
2	0.0963	1	10	0.0087	0.0998	3	30	0.0057	0.1046	3	61	0.0046	0.102	0.003
3	0.0879	6	61	0.0033	0.0884	11	126	0.0031	0.0982	2	23	0.0049	0.089	0.002
4	0.0663	7	80	0.0026	0.0869	12	131	0.0025	0.0834	3	30	0.0034	0.080	0.002
5	0.0664	2	28	0.0052	0.0947	6	76	0.0039	0.0757	2	25	0.0068	0.085	0.003
6	0.0917	2	20	0.0058	0.0886	13	130	0.0032	0.1067	5	50	0.0057	0.093	0.003
7	0.0966	11	110	0.0032	0.0941	20	200	0.0023	0.0939	13	130	0.0026	0.095	0.002
8	0.1280	7	70	0.0052	0.1187	10	104	0.0041	0.1195	9	88	0.0047	0.121	0.003
9	0.1349	11	116	0.0041	0.0909	3	30	0.0103	0.0893	2	20	0.0083	0.121	0.004
10	0.1439	17	170	0.0034	0.1416	16	162	0.0030	0.1189	7	70	0.0054	0.139	0.002
11	0.1568	8	80	0.0054	0.1561	4	39	0.0082	.		0	.	0.157	0.005
12	0.1499	13	170	0.0032	0.1302	17	182	0.0029	0.1419	4	39	0.0081	0.140	0.002
total	0.1105	88	955		0.1085	120	1265		0.1032	50	536		0.113	.001

† There were no sea urchins sampled from fishermen at SCI during January and November.

Table 2. (a) Two-way ANOVA results testing the differences in commercial red sea urchin total effort (number of receipts) and total landings (thousands of kg) during 2009-2011, between management seasons, months with no management restrictions (*unlimited* access) and months with 4-day work weeks (*limited* access) and between the two regions, Channel Islands (14 CDFW blocks) and the port of Fort Bragg. Mean total effort and total landings per management season and region and one standard error are displayed. (b) Effect tests for ANOVAs.

(a)

					CI		FB	
	R^2	$F_{3,23}$	*P*	season	mean	SE	mean	SE
total effort	0.88	48.4	<0.0001	limited (June-Oct)	1325	94	367	47
				unlimited (Nov-May)	1113	79	418	40
total landings	0.83	33.3	<0.0001	limited (June-Oct)	710	62	221	26
				unlimited (Nov-May)	628	53	242	22

(b)

Effect Tests		total effort		total landings	
Source	DF	F Ratio	*P*	F Ratio	*P*
management season	1	1.4	0.2535	0.5	0.4979
region	1	143.8	<0.0001	99.1	<0.0001
management season*region	1	3.7	0.0702	1.4	0.2537

Table 3. Regional variation in commercial fishing data (CDFW) from the Channel Islands (2009-2011): total effort (number of receipts), total landings (kg), mean price per kg (US$), and total value (US$). (a) seasonal variation summary statistics of monthly (n=12) data: mean, standard error (SE), and coefficient of variation (CV), and (b) Regional variation among the three western subregions within the Channel Islands (Fig. 1) ANOVA results, post hoc Student's t-test, and comparing subregion monthly means using percentages (e.g., total effort in the west subregion were 47% greater than the central subregion).

(a)

	west			central			east			Anacapa		
	mean	SE	CV	mean	SE	CV	mean	SE	CV	mean	SE	CV
total effort	631	51	27.8	334	21	21.7	228	12	17.6	8	1	57.6
total landings	366,464	30,758	29.1	188,801	13,360	24.5	104,634	5,810	19.2	2,626	584	77.0
mean price	$1.46	$0.04	9.4	$1.38	$0.04	9.4	$1.27	$0.02	5.5	$2.53	$0.54	74.2
total value	$493,517	$53,143	37.3	$251,213	$23,823	32.9	$130,497	$7,801	20.7	$3,158	$556	61.0

(b)

				Post hoc Student's t-test					
	R^2	F_{DF}	*P*	west	central	east	west > central	west > east	west > mean (central, east)
total effort	0.652	$F_{2,35}$=30.9	<0.0001	A	B	B	--	--	55%
total landings	0.681	$F_{2,35}$=35.3	<0.0001	A	B	C	48%	71%	--
mean price	0.092	$F_{2,35}$=1.7	0.2049	A	A	A	--	--	--
total value	0.591	$F_{2,35}$=23.8	<0.0001	A	B	C	49%	74%	--

Table 4. Regional and seasonal variation in commercial fishing effort and landings (CDFW) from the three western subregions within the Channel Islands (2009-2011): total effort (number of receipts) and total landings (kg) across two seasons (months of lowest [trough: April through June] and highest [peak: September through December] red sea urchin gonadosomatic index). (a) ANOVA results and (b) post hoc Student's t-tests. Highest GSI season per region are highlighted in gray for ease of comparison.

(a)

Response Variable	Effort	Landings
R^2	0.892	0.926
$F_{5,20}$	24.8	37.8
P	<0.0001	<0.0001

Effect Tests		Total effort		Total landings	
Source	DF	F Ratio	*P*	F Ratio	*P*
region	2	37.9	<0.0001	58.3	<0.0001
season	1	20.6	0.0004	30.4	<0.0001
region*season	2	7.9	0.0046	11.9	0.0008

(b)

	Total effort		Total landings				
region, GSI season	LS Mean	SE	LS Mean	SE			
west,highest	862	40	514,576	20,613	A		
west,lowest	470	46	263,765	23,802		B	
central,highest	420	40	241,766	20,613		B	
central,lowest	266	46	148,999	23,802			C
east,highest	261	40	121,816	20,613			C
east,lowest	258	46	118,579	23,802			C

Figures

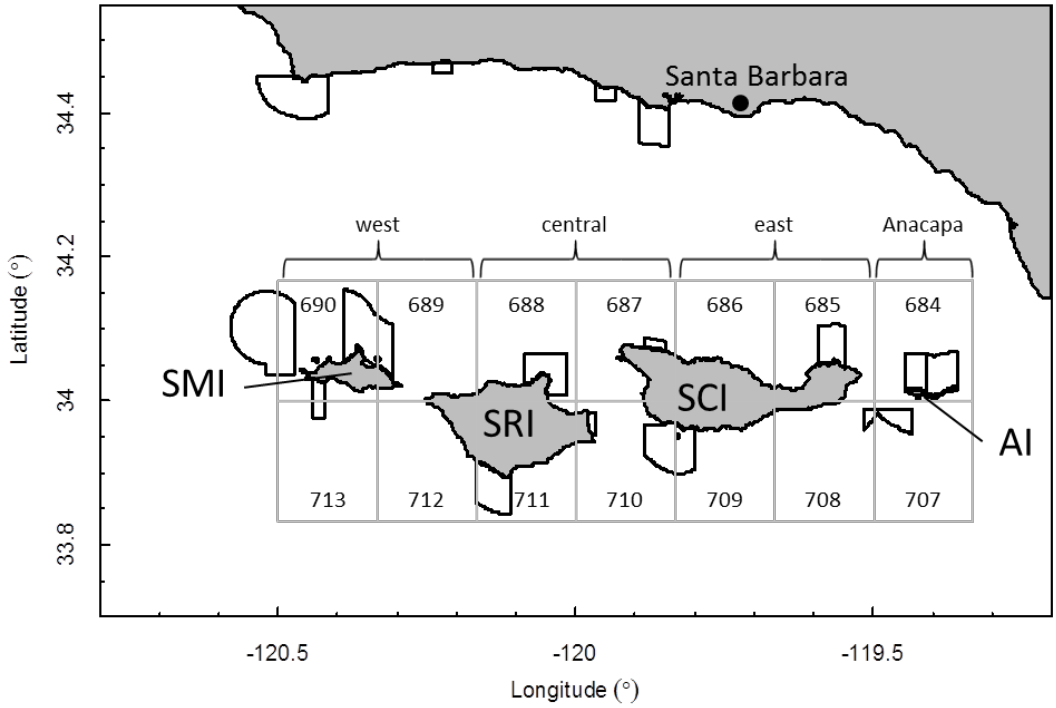
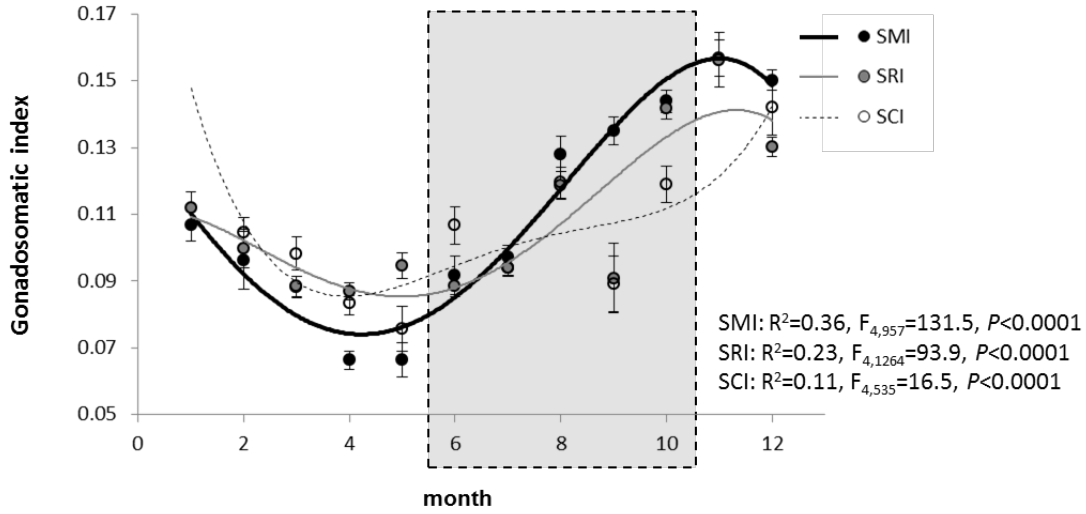


Figure 1. Map of the Santa Barbara Channel with California Department of Fish and Wildlife (CDFW) 10 x 10 nautical mile fishing blocks surrounding the northern Channel Islands from west to east: San Miguel Island (SMI), Santa Rosa Island (SRI), Santa Cruz Island (SCI), and Anacapa Island (AI). All subregions include 4 CDFW 10 x 10 nautical mile blocks, except Anacapa only includes 2 blocks: *west* includes all of SMI and the western tip of SRI, *central* includes the majority of SRI and the western tip of SCI, *east* includes the majority of SCI, and *Anacapa* includes the entire island of Anacapa. Marine reserves are outlined in black.



SMI: GSI = -0.02 + 0.02* month + 0.0009*(month-7.4)^2 - 0.0004*(month-7.4)^3 - 0.00002*(month-7.4)^4
SRI: GSI = 0.002 + 0.01* month + 0.002*(month-7.4)^2 - 0.0005*(month-7.4)^3 - 0.00006*(month-7.4)^4
SCI: GSI = 0.06 + 0.006* month - 0.0005*(month-7.4)^2 - 0.00004*(month-7.4)^3 + .00005*(month-7.4)^4

Figure 2. Monthly mean gonadosomatic index per boat sampled from red sea urchins landed at the port of Santa Barbara from December 2008 to December 2011 per island: San Miguel Island (SMI), Santa Rosa Island (SRI), and Santa Cruz Island (SCI); error bars show one standard error. Lines show the quartic polynomial fits (for viewing purposes only; see Table 1 and Appendix B for statistical analyses) of the monthly means per island. The gray box highlights the months when fishing is limited to four-days per week.

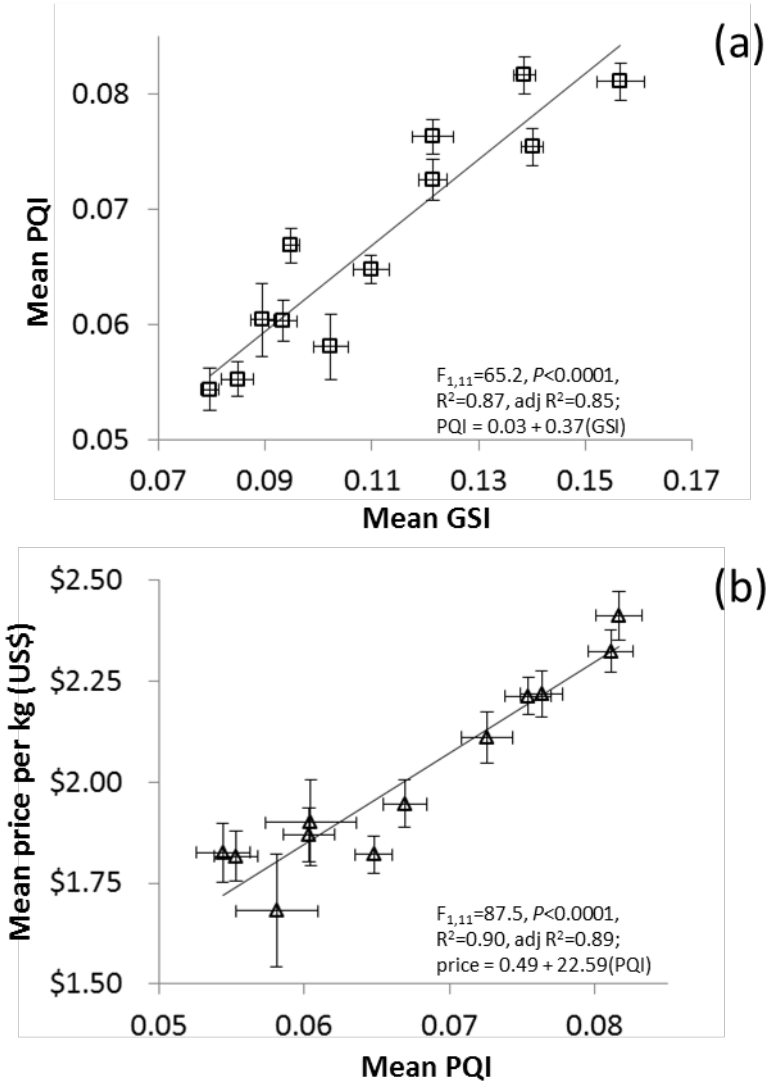


Figure 3. Processor data regressions: (a) mean port-sampling GSI predicting mean PQI and (b) mean processor quality index (PQI) predicting mean processor price per kg (US$). Error bars show one standard error.

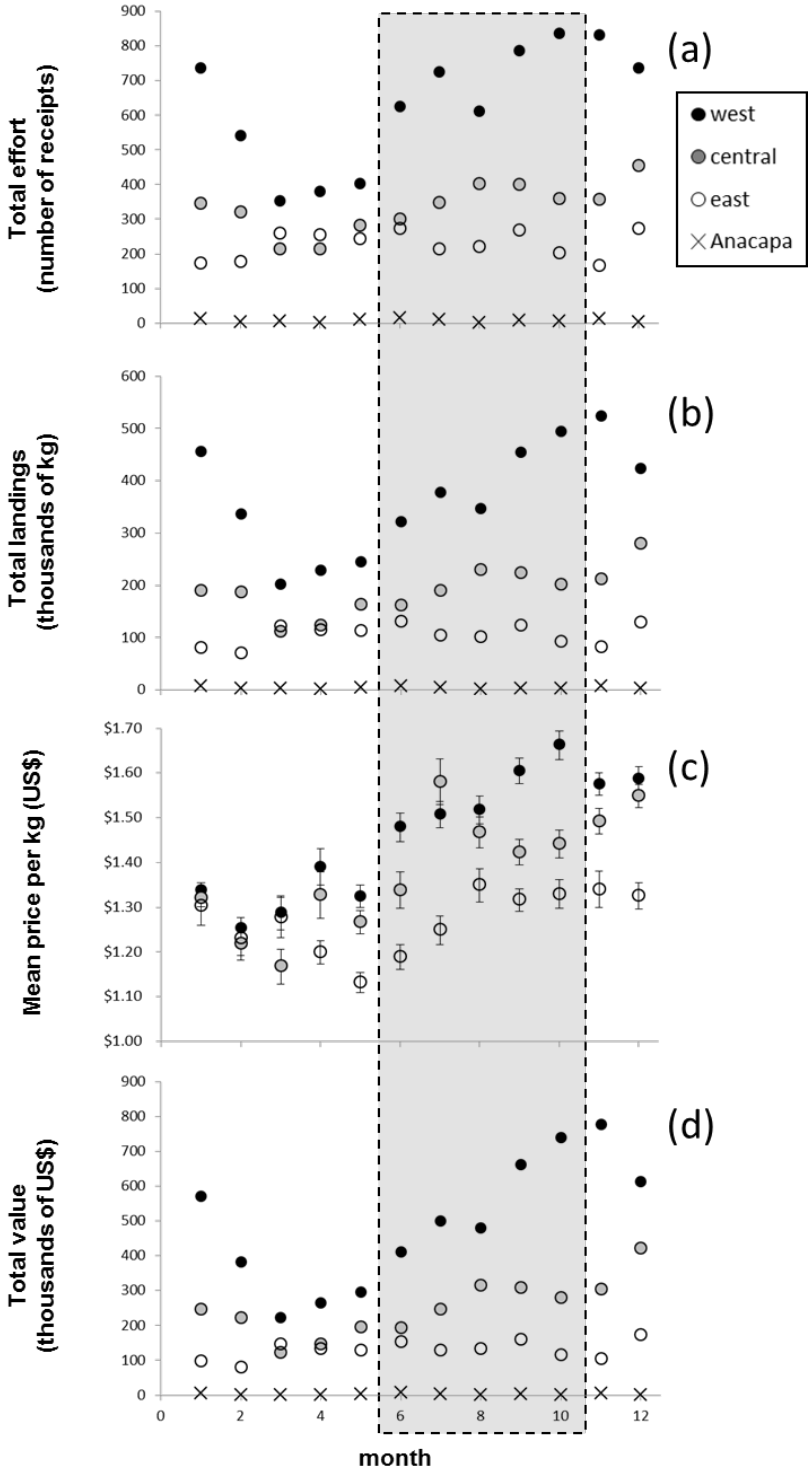


Figure 4. (caption next page)

Figure 4. Monthly data from CDFW in commercial red sea urchin (a) total effort (number of receipts), (b) total landings (thousands of kg), (c) mean price per kg ± one SE (US$), and (d) total value (thousands of US$) for the northern Channel Islands fishery per year (2009-2011). *West* includes all of SMI and the western tip of SRI, *central* includes the majority of SRI and the western tip of SCI, *east* includes the majority of SCI, and *Anacapa* includes the entire island of Anacapa which is minimally fished. All subregions include 4 CDFW 10 x 10 nautical mile blocks, except Anacapa only includes 2 blocks (see Fig. 1). (Note: Anacapa was excluded from plot (c) mean price per kg due to extreme outliers and since less than 1% of the receipts, landings, and value came from Anacapa.) The gray box highlights the months when fishing is limited to four-days per week. Summary statistics are provided in Table 2.

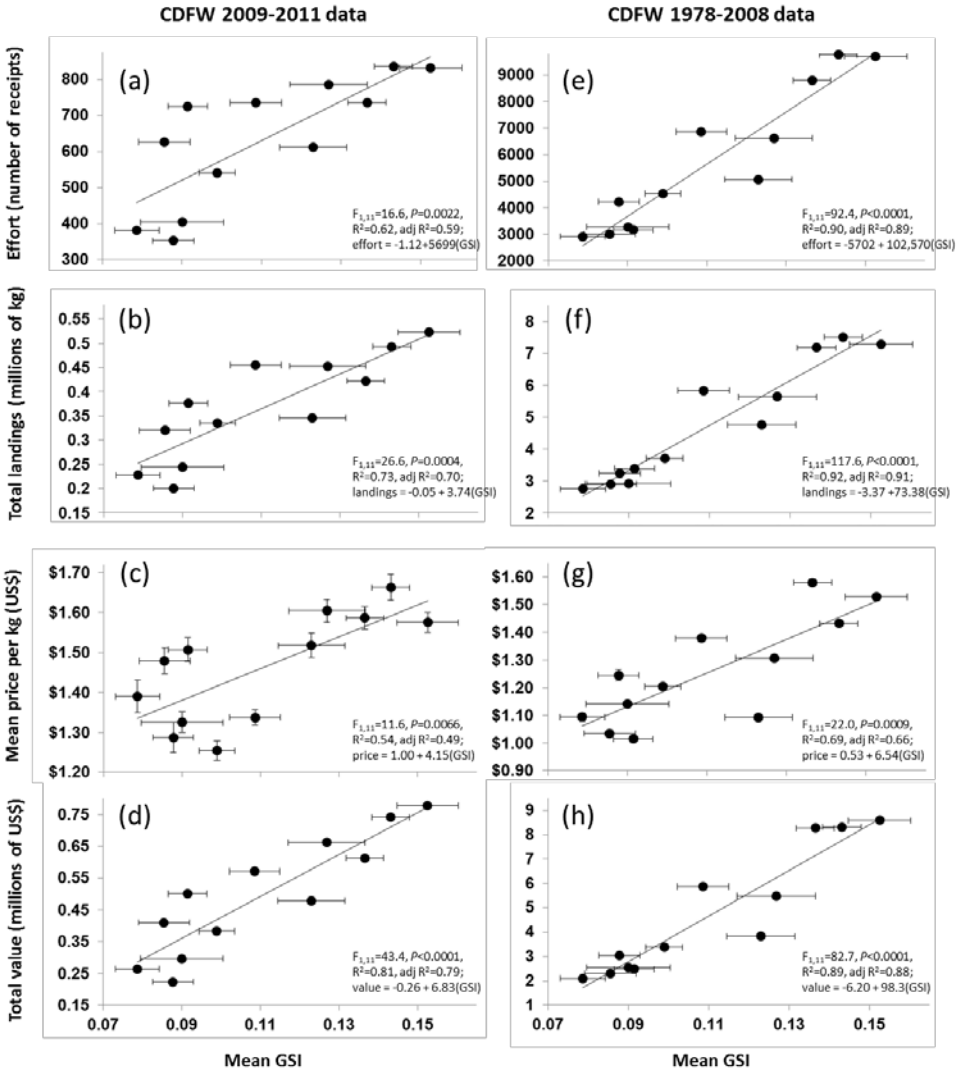


Figure 5. Mean port-sampling gonadosomatic index (GSI) predicting average monthly CDFW data for 2009-2011 and for 1978-2008 in (a, e) effort (number of receipts), (b, f) total landings (millions of kg), (c, g) mean price per kg (US$), (d, h) total value (millions of US$) within the *west* subregion (see Fig. 1). Error bars show one standard error (note: many error bars are smaller than marker size).

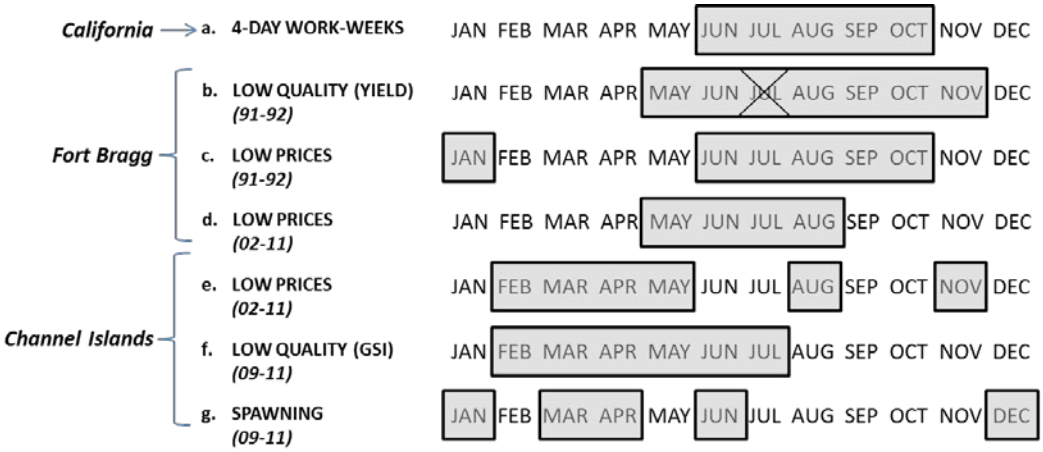


Figure 6. Comparing months across the California sea urchin fishery within Fort Bragg in northern California and the Channel Islands in southern California. Gray highlights: (a) the five months with limited fishing across the state of California (commercial sea urchin fishermen are allowed to fish four-days per week during these months); the rest of the year there is unlimited fishing; (b) the six months with the lowest quality (yield) from a processor in Fort Bragg 1991-1992 (Table C3), the location and time-frame which was examined to establish the four-day work weeks; July is excluded due to the fishery being closed during this period; (c) the six months with the lowest prices in Fort Bragg 1991-1992 (Table C2); (d) the four months with the lowest prices in Fort Bragg 2002-2011 (Table C4), (e) the six months with the lowest prices in the Channel Islands 2002-2011 (Table C1); (f) the six months with the lowest quality in the Channel Islands 2009-2011 (Table B2) and (g) the five months with the highest spawning levels in the Channel Islands 2009-2011(Table B3).

Appendix A
Processor quality evaluation and seasonal processor quality index

The California Sea Urchin Commission developed grade names and guidelines to assist in standardizing uni quality within the industry. “California Gold” is the highest quality, or *grade A* uni, and the gonads have a bright color, firm texture, and are fresh and intact. Sea urchins are graded as “Premium California,” or *grade B* uni, if the gonads are slightly duller in color, firm texture, fresh and mostly intact. Grade A and grade B uni are sold fresh to distributors and restaurants, largely to be consumed raw. “Select California” is also known as *vana*, or grade C; gonads from these sea urchins vary in color (often darker), have softer texture, are watery and are broken in pieces. Vana is usually shipped frozen and makes up about 5-10% of the gonads extracted (D. Rudie, pers. comm.). For each trip per boat, processors in California categorize the sea urchin product within these three grades. Recently retail values of grade A, B, and vana are approximately $225/kg, $158/kg, and $41/kg (or, $102/lb, $72/lb, and $19/lb), respectively as of 2015.

In recent years, grade A is mostly sold in the USA, and grade B is largely exported to Japan (D. Rudie, pers. comm.). Currently about 80-95% of grade A remains in the domestic market and the rest largely is shipped to Japan for auction. However, 30 years ago about 95% of grades A and B was exported to Japan. By volume California exports around 50% of the landings (mostly to buyers in Japan) making up about 10-15% of Japanese supply. However by value only about 25-35% is exported (D. Rudie, pers. comm.).

The sea urchin industry also uses these grades to calculate the overall gonad *yield* to convey a general measure of quality per fishing trip. Yield is often calculated as the percentage of high-grade uni (grades A and B) that was extracted from a fisherman’s load. In other words, from the entire load weighed at the dock, yield is the percentage of uni which is most valuable to the industry. While yield (grades A+B, based on instantaneous qualification) is an important factor the industry uses to set the price of a batch of sea urchins, we investigated whether GSI (based on a quantitative index) can adequately capture the variability in price.

We expected yield to be less than GSI because gonad weight measured by processors is often lower and total weight is often higher for several reasons:

(1) processor gonad weight does not include the vana or any pieces of gonad that were discarded due to low quality or breakage;

(2) processors use the total weight of the sea urchins as the entire load weighed at the dock which occasionally could include undersized sea urchins, purple sea urchins, debris from the sea urchin nets (e.g. other organisms, small rocks attached to the sea urchins, or pieces of kelp);

(3) we weighed the whole weight of sea urchins on an individual basis typically 12-24 hours after collection, when some water weight may have been lost from the sea urchin; and

(4) processors soak gonads in an anhydrous potassium alum, $KAl(SO_4)_2$, solution that will draw some of the water weight out of the gonads. In addition, after soaking in the solution, gonads are placed on towels to soak up any dripping water.

The seasonal processor data showed a fall peak in price per kg and in percent grade A and B of total landings, which roughly matches the November peak GSI (Fig. A1). In addition, we examined processor price records, since in recent years a practice of reporting an arbitrary price in the CDFW landing receipts has resulted in inaccurate CDFW data. Since our analyses with both processor and CDFW price datasets were similar, we used CDFW price data since the sample size was larger. Processor price was the lowest in February. Finally, we examined the pattern of quality across season by calculating the percent grade A and B gonad extracted from the total landings. Percent grade B of the total landings was lowest in April, coinciding with the GSI minimum both in port and processor samples.

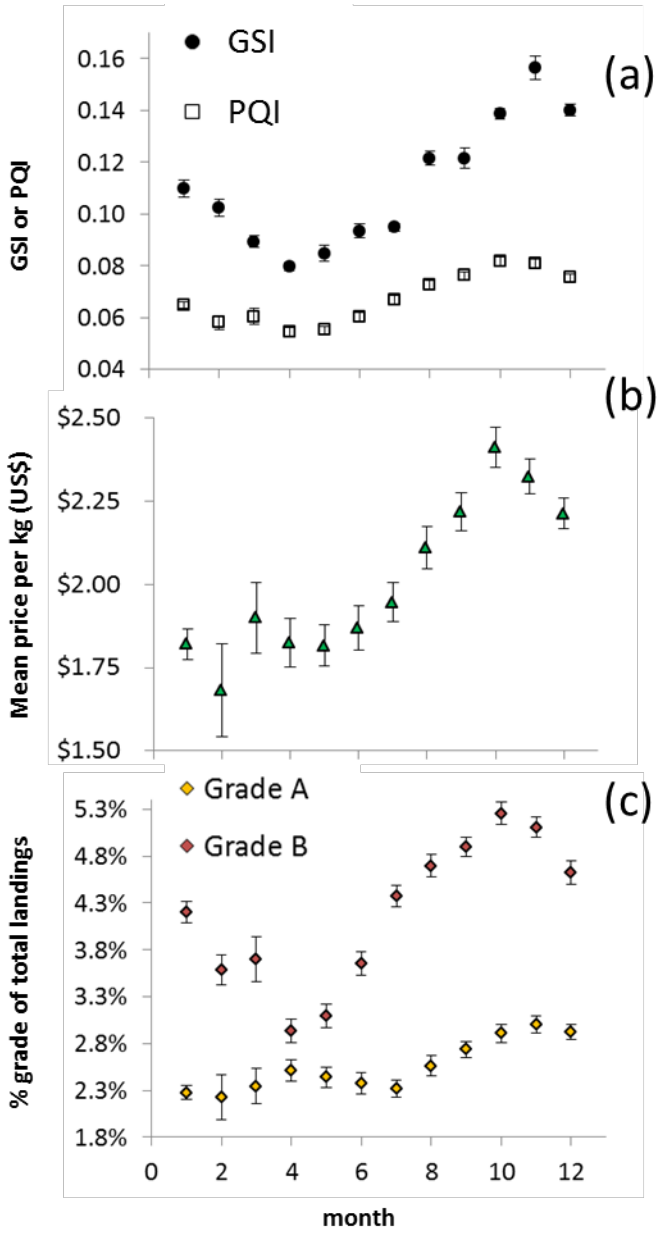


Figure A1. Monthly (a) mean port-sampling gonadosomatic index (GSI) and processor quality index (PQI), and monthly data from red sea urchin data from a processor (b) mean price per kg (US$) and (c) percent grade A and B gonad weight of total landings weight. Error bars for price, GSI, PQI, and percent grade show one standard error (note: many error bars are smaller than marker size). Processor quality index does not include the weight of the *vana* or any gonads that were discarded due to low, unmarketable quality (because these data were unavailable).

Appendix B
Summary of port-sampled red sea urchins and month-to-month within-island and overall differences in GSI and spawning levels

Table B1. For the ten months we had samples from all three islands, summary of red sea urchin gonadosomatic index (GSI) differences across gender, island, and month (a) overall ANOVA effect tests ($F_{30,2496}$=34.7, P<0.0001, R^2=0.30) and (b) post-hoc using Student's t (levels not connected by same letter are significantly different) for month differences and (c) island by month differences.

(a)

Source	DF	F Ratio	Prob > F
gender	1	2.6	0.1075
island	2	0.4	0.6935
month	9	68.6	<0.0001
island*month	18	6.7	<0.0001

(b)

Month							LS Mean	Mean	SE
12	A						0.141	0.141	0.002
10		B					0.135	0.138	0.002
8			C				0.123	0.122	0.002
9				D			0.108	0.123	0.004
2				D	E		0.101	0.103	0.005
6					E		0.096	0.094	0.003
7					E		0.096	0.095	0.002
3					E	F	0.092	0.090	0.003
5						F G	0.085	0.088	0.004
4						G	0.079	0.080	0.003

(c)

Island, month												LS Mean
SMI,12	A											0.151
SMI,10	A	B										0.143
SCI,12	A	B	C									0.142
SRI,10		B										0.142
SMI,9		B	C									0.135
SRI,12			C									0.131
SMI,8			C	D								0.128
SCI,8				D	E							0.120
SRI,8				D	E							0.120
SCI,10				D	E	F						0.119
SCI,6						F	G					0.107
SCI,2							G	H				0.105
SRI,2							G	H	I	J		0.102
SCI,3							G	H	I	J		0.098
SMI,7							G	H	I			0.098
SMI,2					E	F	G	H	I	J		0.097
SCI,7							G	H	I	J		0.096
SRI,5							G	H	I	J		0.096
SRI,7								H	I	J		0.094
SRI,9							G	H	I	J		0.094
SCI,9							G	H	I	J		0.093
SMI,6							G	H	I	J		0.092
SCI,5							G	H	I	J		0.090
SRI,6									I	J		0.090
SRI,3									I	J		0.089
SMI,3									I	J		0.088
SRI,4										J		0.087
SCI,4									I	J	K	0.084
SMI,5											K	L	0.068
SMI,4												L	0.066

Table B2. For January and November, we had samples from only SMI and SRI, summary of red sea urchin gonadosomatic index (GSI) differences across gender, island, and month (a) overall ANOVA effect tests ($F_{3,210}$=22.3, P<0.0001, R^2=0.24) and (b) mean GSI differences.

(a)

Source	DF	F Ratio	Prob > F
gender	1	0.1	0.7548
island	1	0.3	0.6147
month	1	64.6	<0.0001

(b)

Month	Mean	SE
1	0.110	0.004
11	0.158	0.004

Table B3. Summary of red sea urchin port sampling: within-island and overall month-to-month mean gonadosomatic index (GSI) differences: (a) ANOVA results and (b) post-hoc using Student's t (levels not connected by same letter are significantly different).

(a)

	n	R^2	F Ratio	*P*
SMI	955	0.369	50.1	<0.0001
SRI	1265	0.258	39.7	<0.0001
SCI	536	0.161	11.2	<0.0001
Overall	2756	0.272	93.3	<0.0001

(b)

Mo	SMI								Mo	SRI							Mo	SCI							
11	A							0.1568	11	A							0.1561	12	A						0.1419
12	A	B						0.1499	10		B						0.1416	8		B					0.1195
10		B	C					0.1439	12			C					0.1302	10		B					0.1189
9			C	D				0.1349	8				D				0.1187	6		B	C				0.1067
8				D				0.1280	1				D	E			0.1120	2			C	D			0.1046
1					E			0.1068	2					E	F		0.0998	3			C	D	E		0.0982
7					E	F		0.0966	5						F		0.0947	7				D	E		0.0939
2					E	F		0.0963	7						F		0.0941	9			C	D	E	F	0.0893
6					E	F		0.0917	9						F		0.0909	4					E	F	0.0834
3						F		0.0879	6						F		0.0886	5						F	0.0757
5							G	0.0664	3						F		0.0884								
4							G	0.0663	4						F		0.0869								

Mo	Overall							
11	A							0.1566
12		B						0.1399
10		B						0.1386
9			C					0.1215
8			C					0.1215
1				D				0.1098
2				D	E			0.1023
7					E	F		0.0947
6					E	F		0.0934
3						F	G	0.0894
5							G	H	0.0849
4								H	0.0796

Table B4. (a) Summary of gender and presence of spawning from port-sampled red sea urchins per month (2009-2011). Spawning levels are highlighted according to the degree of spawning: 50% or > is light gray, 60% or > is medium gray, and 70% or > is black. Note: presence of spawning was indicated when active spawning was observed during dissections. Some individuals at the spawning stage may have gone undetected, thus these percentages may be biased downward. (b) ANOVA results comparing differences in percent spawning levels per month within each island and overall within the entire region. (c) Post hoc Student's t-test showing monthly differences in spawning levels within the region (levels not connected by same letter are significantly different).

(a)

Month	% female collected	Percent spawning per gender		Percent spawning per island			Overall % spawning
		Female	Male	SMI	SRI	SCI	
1	48%	72%	57%	58%	79%	--	69%
2	55%	39%	44%	10%	20%	56%	29%
3	53%	64%	47%	65%	48%	85%	63%
4	54%	58%	56%	61%	56%	53%	57%
5	59%	46%	50%	36%	57%	17%	37%
6	62%	34%	36%	60%	33%	56%	47%
7	61%	22%	45%	23%	31%	45%	33%
8	59%	16%	38%	24%	22%	31%	26%
9	59%	9%	34%	23%	17%	0%	13%
10	52%	19%	49%	37%	31%	23%	30%
11	53%	23%	48%	36%	29%	--	33%
12	54%	66%	65%	71%	59%	70%	66%
overall	56%						

(b)

Region	SMI	SRI	SCI	Overall
R^2	0.78	0.66	0.69	0.51
F-ratio$_{DF}$	$F_{11,21}$ 3.25	$F_{11,26}$ 2.70	$F_{9,19}$ 2.46	$F_{11,68}$ 5.39
P	0.0369	0.0383	0.0881	<0.0001

(c)

Month						Mean % spawning overall
1	A					69%
12	A					66%
3	A					63%
4	A	B				57%
6	A	B	C			47%
5		B	C	D		37%
7			C	D		33%
11		B	C	D		33%
10			C	D		30%
2			C	D		29%
8				D		26%
9				D		13%

Month						Mean % spawning SMI	Month					Mean % spawning SRI	Month				Mean % spawning SCI
12	A					71%	1	A				79%	3	A			85%
3	A	B				65%	12	A	B			59%	12	A	B		70%
4	A	B	C			61%	5	A	B	C		57%	6	A	B	C	56%
6	A	B	C	D		60%	4	A	B	C		56%	2	A	B	C	56%
1	A	B	C			58%	3	A	B	C	D	48%	4	A	B	C	53%
10		B	C	D	E	37%	6		B	C	D	33%	7	A	B	C	45%
11	A	B	C	D	E	36%	7		B	C	D	31%	8		B	C	31%
5		B	C	D	E	36%	10		B	C	D	31%	10			C	23%
8			C	D	E	24%	11		B	C	D	29%	5			C	17%
9			C	D	E	23%	8				D	22%	9			C	0%
7				D	E	23%	2		B	C	D	20%					
2					E	10%	9			C	D	17%					

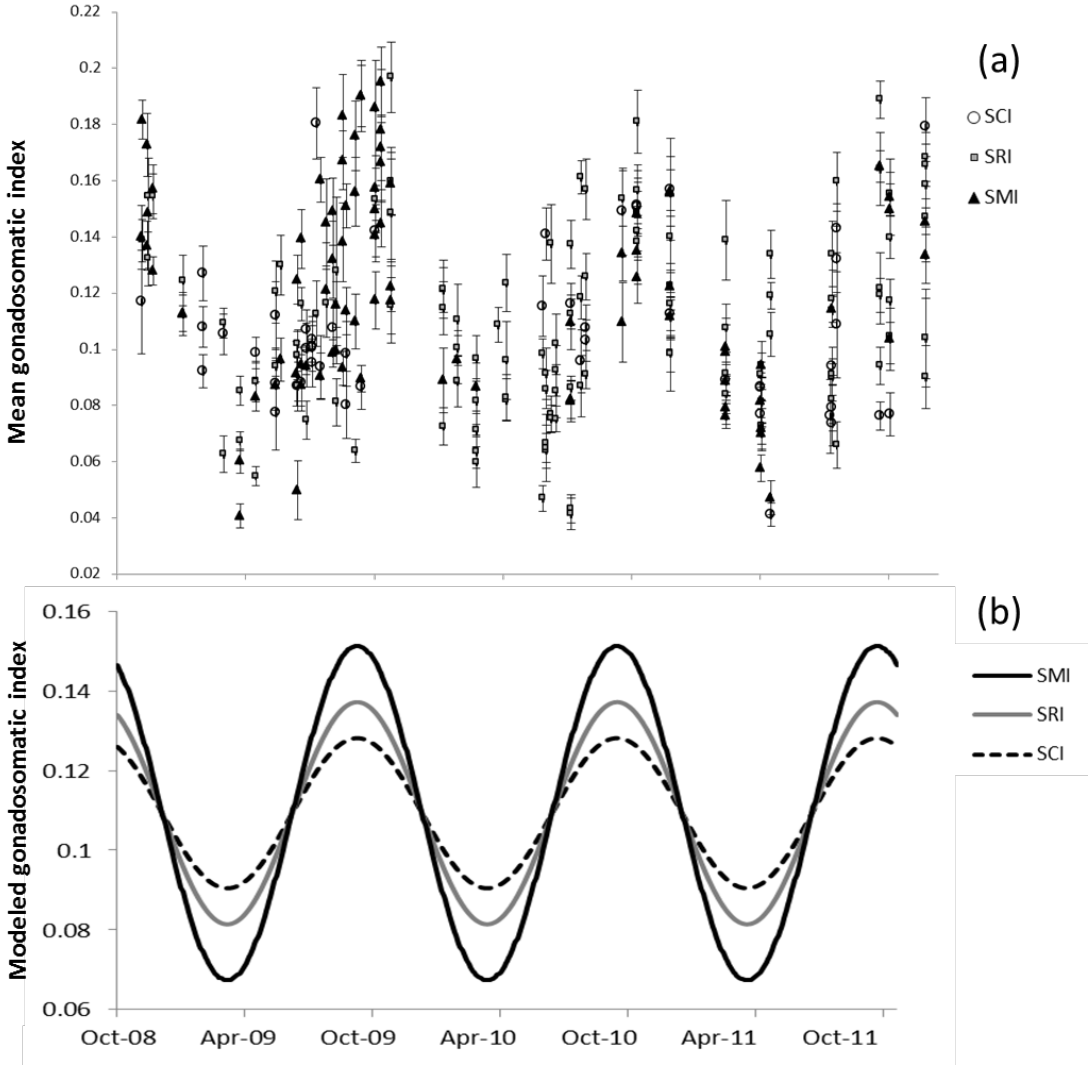


Figure B1. (a) Mean gonadosomatic index (GSI) per boat sampled from red sea urchins landed at the port of Santa Barbara from December 2008 to December 2011 per island: San Miguel Island (SMI), Santa Rosa Island (SRI), and Santa Cruz Island (SCI); error bars show one standard error. (b) Modeled GSI using a sinusoidal function for viewing purposes only.

Appendix C
Monthly variation of red sea urchins

Table C1. Monthly variation in mean price per kg of red sea urchins; post-hoc using Student's t (levels not connected by same letter are significantly different) from ANOVA test ($F_{11,117359}$=52.3, P<0.0001, R^2=0.0048). CDFW data summarized from 2002-2011 from the 14 blocks surrounding the Channel Islands. The six months with the lowest prices are February through April and August and November.

Month								Mean price per kilogram
12	A							$1.63
7		B						$1.59
10		B	C					$1.58
9		B	C	D				$1.57
1			C	D	E			$1.56
6				D	E			$1.55
11					E	F		$1.54
8						F		$1.52
4							G	$1.46
2							G	$1.46
3							G	H	$1.44
5								H	$1.42

Table C2. Monthly variation in mean price per kg of red sea urchins; post-hoc using Student's t (levels not connected by same letter are significantly different) from ANOVA test ($F_{11,8976}$=109.4, P<0.0001, R^2=0.118). CDFW data summarized from 1991-1992 from the port of Fort Bragg, in northern California. This region is where management examined price data (and GSI data) to set reduced effort during the months where prices were the lowest due to low quality. The timeframe examined by management was 1991-1992. The six months with the lowest prices are June through October and January (highlighted in gray).

month									Mean price per kilogram
12	A								2.33
3		B							1.83
2		B							1.82
4			C						1.59
11			C	D					1.49
5			C	D					1.46
1				D	E				1.36
10					E	F			1.24
9						F	G		1.19
6							G	H	1.07
8								H	0.95
7					E	F	G	H	0.51

Table C3. Monthly variation in mean gonad yield of red sea urchins; post-hoc using Student's t (levels not connected by same letter are significantly different) from ANOVA test ($F_{10,496}$=6.84, P<0.0001, R^2=0.123). Data acquired from the CDFW originally from processors in 1991-1992 from Fort Bragg, California (Kalvass and Hendrix 1997). This region is where management examined price data (and GSI data) to set reduced effort during the months where prices were the lowest due to low quality. The timeframe examined by management was 1991-1992. The six months with the lowest yield are highlighted in gray, however there is a lot of overlap in yield among months. July was not included, as the fishery is closed during this month in this location during these years.

Month						Mean gonad yield
1	A	B				10.62
2	A					10.61
3	A					10.52
12	A	B	C			9.87
4	A	B	C			9.70
10		B	C			9.54
11	A	B	C	D		9.40
9			C	D		9.11
5			C	D		8.84
8				D	E	8.14
6					E	7.54

Levels not connected by same letter are significantly different.

Table C4. Monthly variation in mean price per kg of red sea urchins; post-hoc using Student's t (levels not connected by same letter are significantly different) from ANOVA test ($F_{11,12527}$=70.5, P<0.0001, R^2=0.058). CDFW data summarized from 2002-2011 from commercial red sea urchins landing into the port of Fort Bragg. The seven months with the lowest prices are March through September (highlighted in gray).

Month							Mean price per kilogram
12	A						1.67
1		B					1.54
11			C				1.40
2			C				1.40
10			C				1.37
3				D			1.32
9				D			1.32
4				D			1.29
7					E		1.23
6					E		1.21
5					E		1.19
8					E		1.18